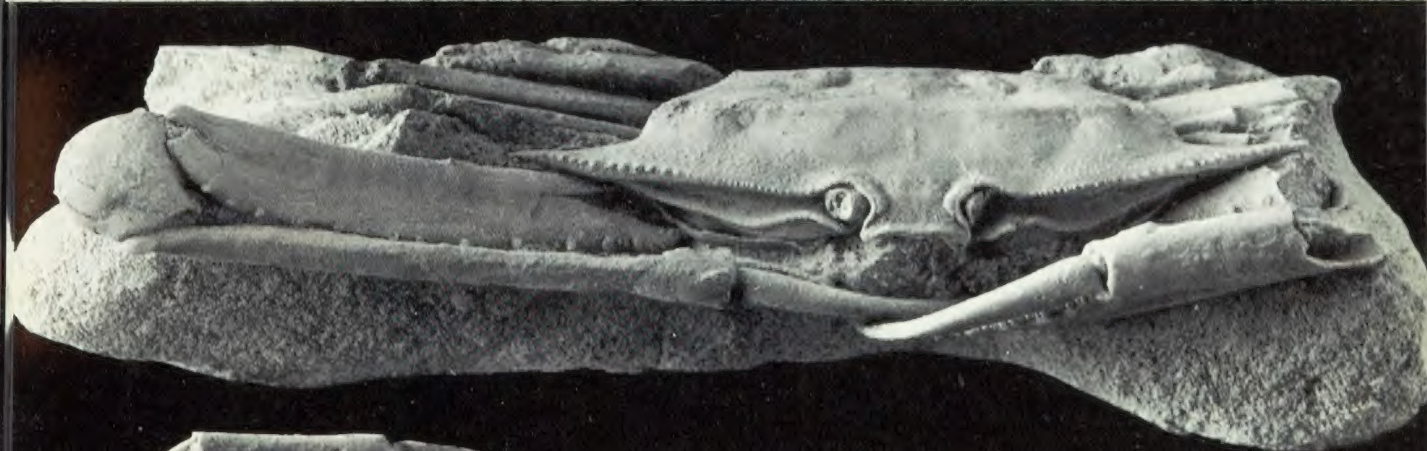


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CONTENTS

PAPERS

VERTEBRATE ZOOLOGY

1. Two new Lizard species from the genus *Leiopisma* (Scincidae: Lygosominae) in south eastern Australia. By P. A. RAWLINSON (Plates 1-2) 1

INVERTEBRATE ZOOLOGY

2. Notes on additions, changes and the distributions of the Australian water bug (Hemiptera-Heteropta). By I. LANSBURY 17
3. The genera *Ophidius* Candèze and *Talganus* gen. nov. (Elateridae: Coleoptera): By A. NEBOISS (Plate 3) 25

PALAEONTOLOGY

4. The fossil crab *Ommatocarcinus corioensis* (Creswell) and a review of related Australian species. By R. J. F. JENKINS (Plates 4-8) 33

AVIAN ZOOGEOGRAPHY

5. Antarctic Dispersal Routes, Wandering Continents and the origin of Australia's Non-passeriform avifauna. By PAT V. RICH 63

TWO NEW LIZARD SPECIES FROM THE GENUS *LEIOLOPISMA* (SCINCIDAE: LYGOSOMINAE) IN SOUTHEASTERN AUSTRALIA AND TASMANIA

By P. A. RAWLINSON

Zoology Department, La Trobe University, Bundoora, Victoria 3083

Summary

Two new species from the genus *Leiopisma* Dumeril and Bibron 1839 are described (*L. coventryi* and *L. greeni*) and earlier literature records of the species are listed. The ecology, distribution and relationships of each species are discussed.

Introduction

Lizards belonging to the genus *Leiopisma* (*sensu* Clarke 1965 and Greer 1970) dominate the cool and cold temperate reptile faunas of Australia. A revision of the genus has almost been completed as part of a survey of temperate Australian reptiles. This survey has involved extensive field collecting and examination of museum collections in Australia and Europe. As a result of the work in museums, all extant type specimens of species which properly belong in the genus *Leiopisma* have been located and examined, thus all described species are known. Recent field collections revealed two new species of *Leiopisma* which were not represented in any European museums and were only poorly represented in Australian museums. Both of the new species are relatively abundant in their rather specialized habitats, one is restricted to montane wet sclerophyll forests in the high rainfall areas of Victoria, the Australian Capital Territory and SE. New South Wales, and the other is restricted to rocky alpine streams and swamps in N. Tasmania. The paucity of museum material can be explained by the fact that these habitats are normally regarded as unsuitable for reptiles and hence collectors have avoided them.

Specimens have been examined from the collections of the Australian Museum, Sydney (AM); the National Museum of Victoria, Melbourne (NMV); Queen Victoria Museum, Launceston (QUM); and the South Australian Museum, Adelaide (SAM). Specimens referred to elsewhere (e.g. Rawlinson 1969 and 1971 as *L. weekesae*) from the collection assembled

while the author was working in the Melbourne University Zoology Department (MUZD) are now all registered in the collection of the NMV.

Genus *LEIOLOPISMA* Dumeril and Bibron 1839

Leiopisma Dumeril, A. M. C., and G. Bibron, 1839, *Erpetologie Generale*, 5: 742-744. Roret, Paris.

Type species (monotypy): *Leiopisma telfairii* Desjardin, J., 1831, *Ann. Scient. Nat.* 22: 292.

The last generic revision was by Mittleman (1952) and his definition of the genus is basically accepted. However, following Clarke (1965) and Greer (1970) the possession of a divided frontoparietal is not regarded as a generic character and consequently the species which Mittleman separated off in the genus *Lampropholis* are included in *Leiopisma*.

There is no doubt that *Leiopisma* as defined here is polyphyletic. Variations in the palatal bone structures of the various species enable the genus to be broken up into two major groups which Greer and Parker (1968) and Greer (1970) have designated as "alpha" and "beta" *Leiopisma*. These morphological groupings correspond to major biological divisions (Rawlinson unpublished), for example all "alpha" *Leiopisma* species are viviparous heliotherms; all "beta" *Leiopisma* species are oviparous and most are also communal nesting thigmotherms. No meaningful attempt can be made to split the genus up at present for details of the morphology and biology of all the present *Leiopisma* species must precede a generic revision, however it can be recorded that the two new species described below are true "alpha" *Leiopismas*.

Diagnosis: Small to moderately large skinks. Limbs pentadactyl, digits not elongate, sub-

digital lamellae undivided. Lower eyelid moveable with a well developed transparent palpebral disc bordered above by the lower ciliaries, otherwise surrounded by small granular scales. External ear opening obvious and tympanum visible. Supranasal and postnasal scales lacking. Prefrontals enlarged but fail to contact on midline. Frontoparietals divided or fused but always separate from the interparietal. Parietals large and contact on the midline. One or more pairs of enlarged nuchals. Preanals only slightly enlarged.

***Leiolopisma coventryi* sp. nov.**

Pl. 1., fig. 1.; Fig. 1.; Pl. 2., fig. 3(a).

Lygosoma (Leiopisma) weekesae (? part) Weekes, H. C., 1928, *Proc. Linn. Soc. N.S.W.* 54: 34-60. Weekes, H. C., 1935, *Proc. Zool. Soc. Lond.* 3: 625-645.

Leiopisma metallica Brazenor, C. W., 1947, *Mem. natn. Mus. Vict.* 15: 156-158.

Leiopisma weekesae (?) Rawlinson, P. A., 1967, *Proc. Roy. Soc. Vict.* 80: 211-224. Rawlinson, P. A., 1969, *ibid.* 82: 113-128. Rawlinson, P. A., 1971, *ibid.* 84: 37-52. Rawlinson, P. A., 1971, *Vict. Yearbook* 85: 11-36. Spellerberg, I. F., 1972, *Oecologia* 9: 23-46. Rawlinson, P. A., 1974, *Pap. Proc. Roy. Soc. Tas.* 107: 153-170. Rawlinson, P. A., 1974, Ch. 11, *Biogeography and Ecology in Tasmania. Monographie Biologicae* 26. The Hague, Junk: 230-269.

Leiolopisma sp. nov. Rawlinson, P. A., 1974, *Mem. natn. Mus. Vict.* 35: 87-96.

Holotype: NMV D 40080, adult male, National Museum of Victoria, Melbourne.

Locality: 2 km N. of Mt. St. Leonard, Victoria, 37°33'S., 145°32'E.

Collectors: A. J. Coventry, P. A. Rawlinson and W. R. Rawlinson.

Date of collection: June 21, 1974.

Description: Snout-vent length 43.5 mm. Length of tail (intact) 66 mm, 151% of S-V length. Total length 109.5 mm. Snout-axilla length 16 mm. Axilla-groin length 24 mm. Length of forelimb 10.5 mm, 24% of S-V length. Length of hindlimb 16 mm, 36% of S-V length. No supranasal or postnasal scales. Rostral and frontonasal in broad contact. Frontal and frontonasal in narrow contact. Prefrontals large, fail to meet; contact the frontonasal, anterior and posterior loreals, first supraciliary, first supraocular and frontal. Anterior and posterior loreals large, subequal. Frontoparietals divided. Interparietal separate,

large, about half the size of the frontoparietals. Parietals large, contact along midline. One very enlarged pair of nuchals followed by a series of smaller pairs. A series of enlarged temporal scales. Four supraoculars, the second the largest (on the right hand side the third has an abnormal division). Six supraciliaries. Seven upper ciliaries, the third, fourth and fifth enlarged and project outwards. Nine lower ciliaries. Lower eyelid moveable with a large transparent palpebral disc bordered above by the lower ciliaries but otherwise surrounded by small granular scales. Length of palpebral disc 0.8 mm. Length of eye 1.7 mm. Seven upper labials, the fifth subocular (on the right hand side abnormal, six upper labials, the fourth subocular). Six lower labials. Ear opening obvious, tympanum visible but partially enclosed as external scales overlap opening. Diameter of external ear opening 0.8 mm. No ear lobules. Ten preanal scales, central pair slightly enlarged. Subdigital lamellae black, undivided and rough, 21 under the fourth toe. Palmar tubercles black, flattened asymmetrically with apical point directed distally. Midbody scales in 26 rows. Dorsal scales with 4 very faint keels. Lateral scales with 3 very faint keels. Ventral scales smooth and highly polished.

Colour in life drab, pattern resembles that of *L. delicata* (unrelated, a "beta" *Leiolopisma*). Dorsal surface of head dark brown with black flecks. Dorsal surface of neck, trunk and tail dark brown, each scale with 3-4 fine black lines which sometimes fuse to give a black patch, many scales with light olive flecks between the black lines. Dorsolateral scales on neck, trunk and anterior section of tail with a light yellow upper half and black lower half giving the impression of a light dorsolateral stripe bordered below by black. This "stripe" extends from the eye onto the tail where it is broken up. Upper lateral scales from eye to anterior section of tail black with scattered brown flecks. Lower lateral scales light grey with scattered black, brown and even yellow flecks. Ventral surface light grey with some scattered black flecks especially under the chin. Palms and subdigital lamellae black.

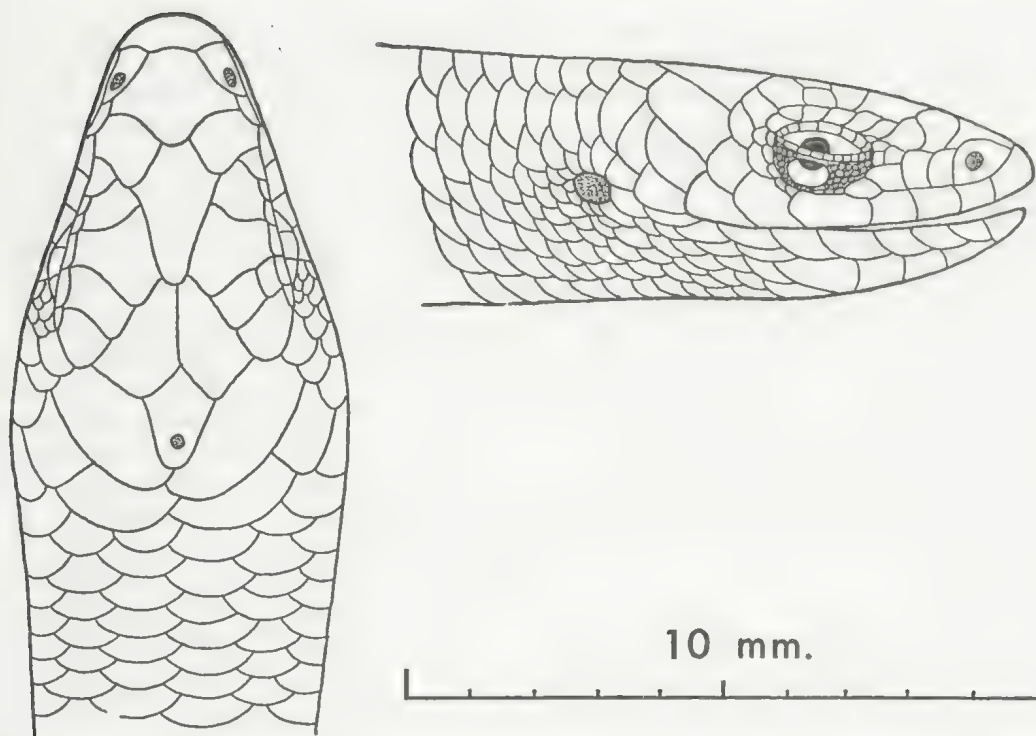


Fig. 1—Headshields of *Leiolopisma coventryi* sp. nov. NMV D40080.

Paratypes: Thirty-five specimens; 28 adult females, NMV D 40081-97, D 40102-112, and 7 adult males, NMV D 40098-101, D 40113-115, National Museum of Victoria, Melbourne.

Locality: 2 km N. of Mt. St. Leonard, Victoria, 37°33'S., 145°32'E.

Collectors: A. J. Coventry, P. A. Rawlinson and W. R. Rawlinson.

Date of collection: June 21, 1974.

Description of the 35 paratypes: As for holotype except as follows: Snout-vent length 35.5-51.0 mm, mean 43.3 mm. Intact tail 124-151% (mean 138%) of S-V length (8 specimens). Total length of adults with intact tails 87.5-109.5 mm, mean 98.2 mm (8 specimens). Length of forelimb 8.5-12.0 mm, mean 10.8 mm; 22-27% (mean 24.7%) of S-V length. Length of hindlimb 12.0-17.0 mm, mean 15.3 mm; 31-39% (mean 34.9%) of S-V length. One very enlarged pair of nuchal scales in 34 of the paratypes, NMV D 40110 has two very enlarged pairs. Six supraciliaries in 33 of the paratypes, NMV D 40086 and NMV D 40100 each have seven. Seven upper labials with the fifth subocular in 34 of the paratypes, NMV D 40114 has six upper labials with the fourth subocular. Lamellae under the fourth toe 19-23,

mean 20.5, mode 20. Midbody scales in 25-27 rows, mean 25.9, mode 26.

Colour of all paratypes as for holotype.

Sexual Dimorphism in the Type Series: There is some evidence of sexual dimorphism, adult males tend to be smaller and longer limbed as the following figures illustrate. As only one male (the holotype) has a complete tail it is not known if there is any relative difference in tail length.

Snout-vent length:

Females 35.5-51.0 mm, mean 44.3 mm
(28 specimens).

Males 36.0-43.5 mm, mean 40.0 mm
(8 specimens).

Length of forelimb:

Females 8.5-12.0 mm, mean 10.9 mm,
22-27% (mean 24.3%) of S-V length
(28 specimens).

Males 9.5-12.0 mm, mean 10.6 mm,
24-27% (mean 26.1%) of S-V length
(8 specimens).

Length of hindlimb:

Females 12.0-18.0 mm, mean 15.4 mm,
31-38% (mean 34.3%) of S-V length
(28 specimens).

Males 13.5-17.0 mm, mean 15.0 mm,
35-39% (mean 36.9%) of S-V length
(8 specimens).

L. coventryi can be easily separated from its closest relatives *L. metallica* and *L. entrecasteauxii* as follows:

1. Frontoparietals undivided *L. metallica*
Frontoparietals divided 2
2. Length of palpebral disc more than half
length of eye, midbody scales in 29-33
rows, light dorsolateral and midlateral
stripes *L. entrecasteauxii*
Length of palpebral disc less than half
length of eye, midbody scales in 25-29
rows, no trace of light dorsolateral or mid-
lateral stripes *L. coventryi*

COMMENT

Three species of skinks, *Leiolopisma coventryi*, *Anotis maccoyi* and *Pseudemoia spenceri*, are virtually restricted to SE. Australian montane wet sclerophyll forests. These species are relatively common in their rather specialized habitats, yet they were completely overlooked by the early European collectors who probably avoided densely forested areas. Two of the species, *A. maccoyi* and *P. spenceri*, were described by Lucas and Frost (1894) in "The Lizards Indigenous to Victoria". *L. coventryi* however remained unknown, no specimens were held in the major European museums (Rawlinson unpublished) and by 1894 when Lucas and Frost published their work, only one specimen was preserved in any of the museum collections in Australia (AM R 560). Between 1894 and 1947 one more specimen was added to the AM collection and seven specimens were catalogued into the NMV collection. Thus there was little chance of taxonomists picking up the species prior to 1947. Since 1947 10 specimens have been added to the AM, 193 to the NMV, and 10 to the SAM. These figures help to explain why *L. coventryi* has only been discovered recently. *L. coventryi* is sympatric with its closest relatives, *L. entrecasteauxii* and *L. metallica* in several localities, e.g. the type locality, without hybridizing, thus they are good biological species (*sensu* Mayr 1963).

The present author was responsible for the

name *Leiolopisma weekesae* being applied to *L. coventryi*, and this mistake arose as follows. In 1929 Kinghorn described a new species, *Lygosoma (Liolepisma) weekesae*, which was named after Dr H. C. Weekes. Dr Weekes (1929) described the placentation of a species she ascribed to *L. (L.) weekesae* in an article immediately following Kinghorn's description of that species. After Rawlinson (1974c) *L. (L.) weekesae* is now known to be a junior subjective synonym of *Pseudemoia spenceri*, this was not discovered earlier as Kinghorn stated and illustrated that supranasal scales (diagnostic for *P. spenceri*) were absent in *L. (L.) weekesae*, where in fact they were present and obvious in all his type specimens. However, Weekes' specimens ascribed to *L. (L.) weekesae* could not have all been *P. spenceri*, for the recorded litter sizes (3-7) are much too large for the latter species where litters average 1.9 and range from 1-3. When *L. coventryi* was discovered it was realized that it did not fit any of the early descriptions of *Leiolopisma* species. However, it did fit Kinghorn's description of *L. (L.) weekesae* in all respects except midbody scale counts and the litter size (1-7, mean 3.0) agreed with Weekes' account of the species. In an attempt to identify *L. (L.) weekesae*, collections were made from the localities mentioned by Kinghorn and Weekes, these yielded specimens of *P. spenceri* and *L. coventryi*. Mislead by Kinghorn's inaccurate description, and the litter sizes recorded by Weekes, the author in 1967 tentatively applied the name *Leiolopisma weekesae* to specimens now properly identified as *L. coventryi*. Although dubious about the identification the author has continued to apply the name for the sake of consistency. During work on a revision of the genus *Pseudemoia* (Rawlinson 1974c) the author located all the specimens mentioned in the description of *L. (L.) weekesae* and all proved to be conspecific with *P. spenceri*. Thus the name *L. weekesae* cannot now be associated with *L. coventryi* except for the specimens used in Weekes' work and specimens misidentified by the author (see synonymy above) including the specimens worked on by Spellerberg (1972).

The species is named in honour of John Coventry, Field Officer in the National Museum of Victoria, in recognition of his help in gathering the material presented here and also for his many outstanding contributions to Australian herpetology. He has worked on the NMV amphibian and reptile collections since 1953 and has been responsible for them since 1957. During this period he has completely revised and greatly extended the herpetological collections so that they now rank as one of the best repositories of Australian material and they include the best collections of SE. Australian, Bass Strait and Tasmanian material.

OTHER SPECIMENS EXAMINED

In order to determine the intraspecific variation in some important taxonomic characters, a further 107 specimens including juveniles were examined in detail.

Size: Mature adults: Snout-vent length 35.0-57.0 mm, mean 44.2 mm (76 specimens). Intact tail 118-146% (mean 136%) of S-V length (16 specimens). Total length of adults with intact tails 81.0-113.0 mm, mean 99.1 mm (16 specimens). Juveniles at birth: Snout-vent length 17.0-19.0 mm, mean 18.0 mm (8 specimens). Intact tail 110-127% (mean 114.9%) of S-V length (8 specimens). Total length of juveniles with intact tails 37.0-41.0 mm, mean 38.8 mm (8 specimens).

Scalation: Supranasals and postnasals absent in all specimens examined. Midbody scales in 25-29 rows, mean 27.2 (97 specimens). Lamellae under the fourth toe 16-23, mean 19.2 (97 specimens).

Colour: Remarkably uniform, as for holotype and paratypes above.

The localities and registered numbers of all other specimens of *Leiopisma coventryi* examined are listed below.

New South Wales: (AM) Blue Mountains: South Bowenfels district, R 27022. Black Range: 8 km N. of Jenolan Caves, R 39106; 3 km N. of Jenolan Caves, R 39103-5; Mt. Edwards, Boyd Plateau via Jenolan, R 31595. Snowy Mountains: Island Bend, Mt. Kosciusko National Park, R 15934; Mt. Kosciusko, 1080-1800 m, R 560. (NMV) Black Range: 4 km

WSW. of Jenolan Caves, D 38180-1; 8 km WSW. of Jenolan Caves, D 39189. Snowy Mountains: 5 km ESE. of Laurel Hill, D 32968; Hansens Mill, 23 km S. of Batlow, D 32951; 4 km N. of Cabramurra, D 32969; 6.5 km SW. of Eucumbene, D 32940-5; Sawpit Creek, Mt. Kosciusko Road, D 16728; 8 km ENE. of Thredbo, D 32922; Cascade Creek, 16 km N. of Tin Mine Huts, D 32996. Coast Range: Brown Mountain, D 16729-31, D 32988; 3 km ESE. of Brown Mountain, D 16727.

Australian Capital Territory: (AM) Brindabella Ranges: Brindabella Ra., R 15304, R 15306, R 15343. (NMV) Brindabella Ranges: Picadilly Circus, D 32999; 1.5 km S. of Bulls Head, D 16726.

Victoria: (AM) Victoria, R 4893. (NMV) Burrowa Massif: 1.5 km SE. of Mt. Burrowa, D 17523. Strathbogie Ranges: S. slopes of Mt. Buggaree, Warrenbayne Plantation area, D 17247; Police Track, Warrenbayne Plantation area, D 17167; Albert Track, Warrenbayne Plantation area, D 17229-33, D 17132, D 17741; 1 km WNW. of Junction Police and Albert Tracks, Warrenbayne Plantation area, D 17254-6; Mt. Albert, Warrenbayne Plantation area, D 17733; Chapmans Lane, Warrenbayne Plantation area, D 18027. Blue Range: Whiskey Creek, 13 km SSE. of Tatong, D 18111; The Bird Reserve, D 17393-4; Engelkes Track, between Holland Creek and Spring Creek Road, D 17435; Engelkes Track, between Holland Creek and Old Tolmie Road, D 17432-3. Australian Alps: 4 km SSW. of Cowombat Plain, D 32995; 1.5 km NW. of Mt. Cobberas, D 32981; Limestone Creek, 13 km W. of Mt. Cobberas, D 32997-8; Native Dog Plain, 7 km SW. of Mt. Cobberas, D 32979, D 33397; 3 km N. of Wulgulmerang, D 32946-50; Honeysuckle Track, Currie Creek, 6 km NW. of Gelantipy, D 7728. Coast Range: 21 km ENE. of Mt. Ellery, 790 m, D 14107; 13 km ENE. of Mt. Ellery, 1200 m, D 14151; 9.5 km NE. of Mt. Ellery, D 14162-7; 3 km NE. of Mt. Ellery, D 14173; Yalmy Road, 8 km W. of Goongerah, D 32973. Grampians Range: 3 km SE. of Mt. Victory, D 38184-5; Strachans Camp, D 32926. Western Highlands, Midlands Range: Mt. Cole Forest, 14.5 km S.

of Elmhurst, D 32928; 9.5 km WSW. of Trentham, D 32982; Mt. Blackwood area, D 32952-4. Eastern Highlands including the Victorian Alps: King Parrot Creek, 16 km N. of Kinglake West, D 32955-6; No. 1 Camp, Mt. Disappointment Forest, D 32974, D 33299; 3 km E. of No. 1 Camp, Mt. Disappointment Forest, D 32978; Kilmore Reservoir, 4 km WNW. of Mt. Disappointment, D 32983-90; Mt. Disappointment, D 13970-1, D 32966, D 32991-3, D 40130; 9 km NNE. of Kinglake, D 32957; 15 km N. of Big River Camp, D 32972; 9 km SE. of Marysville, D 32927; 8 km SW. of Lake Mountain, D 38456; 3 km NE. of Mt. St. Leonard, D 32934-5; Mt. St. Leonard, D 32929-33; Blacks Spur, 13 km ENE. of Healesville, D 1737-8; Acheron Gap, Acheron Way, 13 km SSE. of Narbethong, D 33646; Pantons Gap, 11 km SE. of Healesville, D 32920-1; Don Gap, 16 km ESE. of Healesville, D 32936-7; 6 km S. of Kel Junction, D 32925; Mt. Baw Baw, D 11245; 4 km SW. of Mt. Baw Baw, D 13583-4, D 13600; Neulynes Mill, 5 km SW. of Mt. Baw Baw, D 13585; Waterloo, Gippsland, D 1054-5. Dandenong Ranges: Kalorama, D 32967, D 32970-1, D 32975-7, D 33000-6, D 38183; Sassafras, D 1288; Belgrave, D 32939; Emerald, D 2170. Otway Ranges: Kawarren, D 13636; Gellibrand River, Gellibrand, D 12274, D 18022; 5 km S. of Forrest, D 32963; Mt. Sabine, D 13631-5, D 32994; 3 km S. of Wyclangta, D 12242; 3 km N. of Cape Horn, D 32962; 3 km SW. of Cape Horn, D 32923-4; 5 km SW. of Cape Horn, D 32938; 5 km ENE. of Hordern Vale, D 32958-61; Apollo Bay, D 32964-5; 1.5 km NNW. of Blanket Bay, D 38182. Victoria, D 1728. (SAM) Grampians Range: 9 km SE. of Glenisla, 37°17'S., 142°16.5'E., R 13671; 10 km SE. of Glenisla, 37°17'S., 142°17.5'E., R 13672 a-c (3 ex.); 11 km E. of Mooralla, 37°23.5'S., 142°15'E., R 13795 a-c (3 ex.). Otway Ranges: Otway Ra., R 12377; Erskine Falls, 8 km NW. of Lorne, R 12376. South Melbourne (?), R 6197.

DISTRIBUTION

Highlands of SE. New South Wales, Australian Capital Territory and Victoria from the Bowenfels area, Blue Mountains (N.S.W.), to

the Victoria Range in The Grampians (Vic.). The species occurs disjunctly in a number of isolates within this area.

HABITAT

Found only in regions of high rainfall (more than 75 cm per year). Populations within these regions are restricted to large decaying fallen trees, logs or tree stumps in clearings in montane wet sclerophyll forests. The exposed surfaces of the decaying wood are used for basking and foraging sites during activity, while crevices in the wood are used for shelters when inactive.

ECOLOGY

The distribution of *L. coventryi* parallels that of *Pseudemoia spenceri* to a remarkable extent (see map in Rawlinson, 1974c), this is because both species are limited to true montane wet sclerophyll forests. *L. coventryi* also resembles *P. spenceri* in that it is an insectivorous skink with a thermoregulatory behaviour pattern during activity which classifies it as a shuttling heliotherm (see discussions in Rawlinson 1974a, b, c). However, *P. spenceri*, a very agile lizard, is mainly arboreal and most activity is carried out on elevated surfaces, whereas *L. coventryi* is restricted in its activity to logs and litter at or close to ground level (within 1-2 m).

The densest *L. coventryi* populations are found in naturally burnt regenerating montane forests or regenerating montane forests where limited selective cutting for timber has been carried out. In these areas are found the clearings and large decaying fallen trees, logs and tree stumps which provide the essential habitat requirements for basking, foraging and shelter. Some of the densest populations occur in areas where limited selective cutting has been carried out, however the modern forestry management practice in montane forests (Ashton 1956; Butler 1971; Cunningham 1960; Grose 1957), where large areas are clear cut and the slash is later burnt to establish a seed-bed for dense regeneration, destroys the species habitat (sunlit clearings, fallen logs and litter) and eliminates the species from such areas.

Details of hibernation are reasonably well known, in fact the type series collected on June 21, 1974 were all taken from hibernation

sites. When inactive the lizards utilize crevices inside large decaying logs usually only 5-20 cm beneath the surface and within 2 m of ground level. The lizards may hibernate singly, but are more commonly found in dens which may contain up to 8 individuals. This denning probably results from a number of individuals locating the same favourable site rather than from a social factor for other species of skinks are also found in the dens. During the collection of the 36 type specimens, 3 *Leiolopisma entrecasteauxii*, 5 *L. metallica* and 4 *Sphenomorphus tympanum* specimens were also taken from *L. coventryi* dens. The winter hibernation sites of *L. coventryi* make the species very vulnerable to another modern forestry practice, the deliberate lighting of so-called controlled fires in winter for fuel reduction (see for example Hodgson 1969). These fires burn slowly and intensely at ground level setting fire to the logs and litter. Thus the hibernation sites of this species are actually the target of such winter forestry management practices.

Laboratory measurements of the thermal preferences and "Normal Activity Range" of *L. coventryi* have been made from continuous recordings of body temperature in a photo-thermal gradient (15-50°C.) using the methods outlined by Rawlinson (1974c) for *P. spenceri*. These results are summarized in Table 1. As with *P. spenceri*, the specimens in the gradient mirrored their thermoregulatory behaviour in the field, i.e. shuttled continuously from under the radiant heat lamp to shaded cool areas and back. From body temperature measurements made at one-minute intervals on 7 specimens (1136 observations) it was determined that the "Mean Preferred" body temperature was 30.1°C., while the "Voluntary Minimum" and "Voluntary Maximum" body temperatures were 22.7°C. and 37.5°C. respectively (Table 1). The histogram of frequency of body temperature maintained during activity (1°C. class intervals, range 20°-37°C.) is slightly skewed towards the high temperature end of the scale. The mode is the 28°C. class interval, but it is not pronounced and contains only 10% of the observations, while each of the class intervals from 27°-34°C. contain more than 8% of the observations. This result reflects the shuttling

method of thermoregulation with the consequent rapid fluctuations in body temperature as the lizard moves to and from the basking site. The method of thermoregulation also explains the wide range of body temperatures tolerated during normal activity.

Spellerberg (1972) determined the physiological thermal tolerances of the species (as *L. weekesae*, see above) by measuring the "Critical Maximum" and "Critical Minimum" body temperatures. These are the temperatures at which locomotory ability is lost as measured by the loss of the righting reflex. The "Critical Maximum" is 41.9°C. and the "Critical Minimum" is 3.5°C. Thus *L. coventryi* has wide thermal tolerances; it tolerates large fluctuations in body temperature during voluntary activity, the mean normal activity range for the specimens tested was 14.8°C. (22.7°-37.5°C.), the absolute range was 17.6°C. (20.2°-37.8°C.); and specimens are capable of co-ordinated movements over a very wide range of body temperatures, a mean range of 38.4°C. (3.5°-41.9°C.) and an absolute range of 38.9°C. (3.0°-41.9°C.). *Pseudemoia spenceri* which occupies the same major habitat as *L. coventryi* also has very wide thermal tolerances (Rawlinson 1974c).

REPRODUCTION

L. coventryi is a live-bearing skink. There is no trace of eggshells around developing embryos, so it is assumed the species is fully viviparous (i.e. placental). Pregnant females kept under observation in the laboratory produced litters between January 30 and February 13. In all, 15 pregnant females were examined, litter sizes ranged from 1-7 and the mean number of offspring was 3.0 (Table 1). Copulation and the insemination of females takes place in autumn (April). The females store the sperm over winter, ovulation occurs in spring (mid October) and the ova are then fertilized.

Weekes (1929, 1935) described in detail the placentation of a species which was ascribed to *Lygosoma* (*Liolepisma*) *weekesae* but was almost certainly *L. coventryi* (see above). Weekes recorded 3-7 embryos for the specimens she examined which were collected in

TABLE 1

Thermal tolerances and reproduction of *Leiolopisma coventryi* sp. nov.

Body Temperature Value/Litter Size	Number of Observations	Mean	Range
<i>Thermal tolerances:</i>			
Critical Minimum Temperature °C.	2	3.5	3.0-4.0
Voluntary Minimum Temperature °C.	7	22.7	20.2-27.0
Mean Preferred Temperature °C.	1136	30.1	—
Voluntary Maximum Temperature °C.	7	37.5	37.3-37.8
Critical Maximum Temperature °C.	2	41.9	41.9-41.9
<i>Reproduction:</i>			
Litter Size	15	3.0	1-7

the Jenolan area where *L. coventryi* is reasonably common and so it is almost certain that her detailed account of placentation in the species ascribed to *L. (L.) weekesae* applies instead to *L. coventryi*.

RELATIONSHIPS OF *LEIOLOPISMA COVENTRYI*

The palatal bone structure shows that *L. coventryi* is an "alpha" *Leiolopisma* species. As was mentioned by Rawlinson (1974c), there are two groups in "alpha" *Leiolopisma*, viz. species with low midbody scale counts (20-32) which includes *L. entrecasteauxii* and *L. metallica* in Australia, and species with high midbody scale counts (38-66) which includes *L. greeni* sp. nov., *L. ocellata* and *L. pretiosa*. *L. coventryi* has 25-29 midbody scale rows and its closest relatives are undoubtedly *L. entrecasteauxii* and *L. metallica*. It is considered that *L. coventryi* is a sibling species of *L. metallica*.

Leiolopisma greeni sp. nov.

Pl. 1., fig. 2.; Fig. 2.; Pl. 2., fig. 3(b).

Leiolopisma pretiosum (Form B) Rawlinson, P. A., 1971, *Proc. Roy. Soc. Vict.* 84: 37-52.

Leiolopisma sp. nov. Rawlinson, P. A., 1974, Ch. 11, *Biogeography and Ecology in Tasmania, Monographie Biologicae* 26. The Hague, Junk: 230-269.

Holotype: NMV D 18243, adult female, National Museum of Victoria, Melbourne.
Locality: Mt. Barrow summit, 1413 m, Tasmania, 41°23'S., 147°25'E.

Collectors: M. O. Rawlinson and P. A. Rawlinson.
 Date of collection: January 31, 1967.

Description: Snout-vent length 50.0 mm. Length of tail (regrown) 49.0 mm. Total length 99.0 mm. Snout-axilla length 19 mm. Axilla-groin length 29 mm. Length of forelimb 15.0 mm, 30% of S-V length. Length of hindlimb 21.0 mm, 42% of S-V length. Supranasals partially separated off on both sides. No postnasal scales. Rostral and frontonasal in narrow contact. Frontal and frontonasal just in contact. Prefrontals large, narrowly separated; contact the frontonasal, anterior and posterior loreals, first supraciliary, first supraocular and frontal. Anterior and posterior loreals large, subequal. Frontoparietals fused. Interparietal separate, large, about one quarter the size of the frontoparietals. Parietals large, contact on the midline. One enlarged pair of nuchal scales, all other neck scales small. A series of enlarged temporal scales. Four supraoculars, the second the largest. Seven supraciliaries. Six upper ciliaries, the third, fourth and fifth enlarged and project down and outwards. Ten lower ciliaries. Lower eyelid moveable with a large transparent palpebral disc bordered above by the lower ciliaries, but otherwise surrounded by small granular scales. Length of palpebral disc 1.0 mm. Length of eye 2.6 mm. Eight upper labials, the sixth subocular. Eight lower labials. Ear opening obvious, tympanum visible. Diameter of external ear opening 1.1 mm.

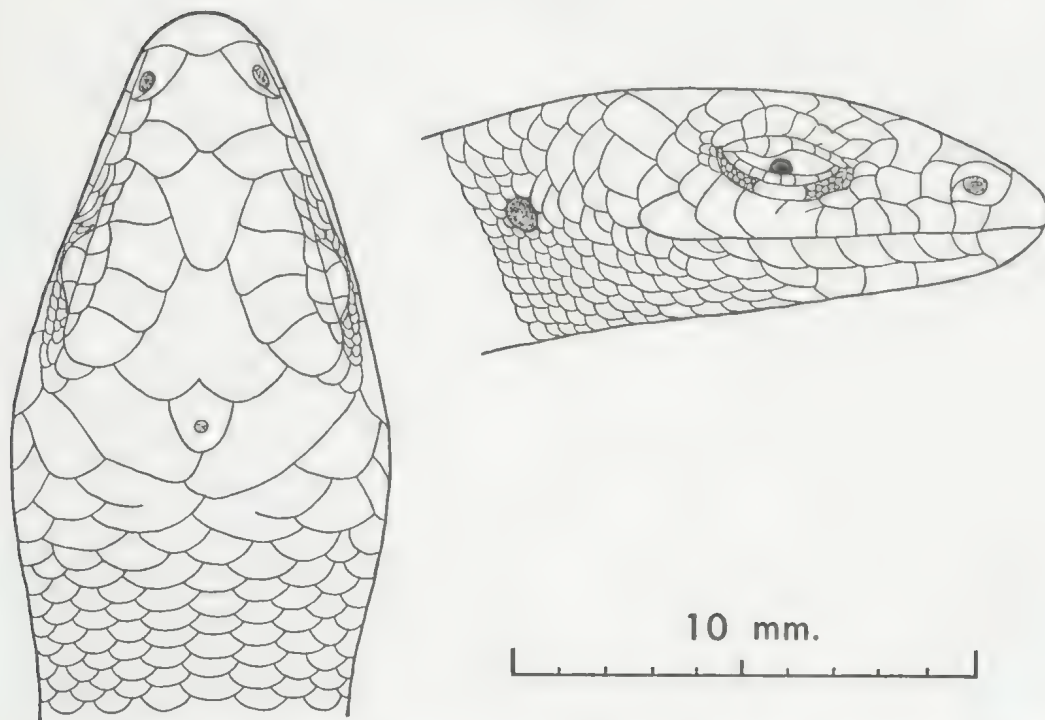


Fig. 2—Headshields of *Leiopisma greeni*, sp. nov. NMV D18243.

Three small anterior ear lobules. Eleven pre-anal scales, central scale slightly enlarged. Subdigital lamellae undivided, smooth, 24 under the fourth toe. Palmar tubercles flattened asymmetrically with apical point directed distally. Midbody scales in 42 rows. Dorsal scales with 3 very faint keels. Lateral scales with 2 very faint keels. Ventral scales smooth.

Colour in life, dorsal surface of head, trunk and tail black, most scales with a grey-green central patch. No dorsolateral stripe. Upper and lower lateral surfaces the same as dorsal surface except grey-green patches enlarge towards the ventral surface. Ventral surfaces grey-green, some black patches along the sides. Palms and subdigital lamellae dark grey.

Paratypes: Sixteen specimens in the collections of the National Museum of Victoria, Melbourne (NMV), the Queen Victoria Museum, Launceston (QVM), and the South Australian Museum, Adelaide (SAM).

NMV D 18240, adult female.

Locality: Mt. Rufus, 1417 m, Tasmania, 42°08'S., 146°06'E.

Collector: J. A. Owen.

Date of collection: February, 1962.

NMV D 18241, D 18244-5, 3 adult females; NMV D 18246-8, 3 adult males; NMV D 18249, juvenile. Locality: Pine Lake, 1150 m, 5 km NNE. of Berona, Tasmania, 41°35'S., 146°43'E.

Collectors: M. O. Rawlinson and P. A. Rawlinson. Date of collection: January 30, 1967.

NMV D 18242, adult female.

Locality: Mt. Barrow summit, 1413 m, Tasmania, 41°23'S., 147°25'E.

Collectors: M. O. Rawlinson and P. A. Rawlinson. Date of collection: January 31, 1967.

QVM 1947.3.4 a-e, three adults and two half-grown specimens, sex not determined.

Locality: Ben Lomond Central Plateau, 1500 m, Tasmania, 41°35'S., 147°39'E.

Collector: M. Merrilees.

Date of collection: January, 1947.

QVM 1972.3.201, half grown, sex not determined. Locality: Ben Lomond summit, 1573 m, Tasmania, 41°32'S., 147°39'E.

Collector: R. Upson.

Date of collection: March, 1971.

SAM R 11136, adult, sex not determined.

Locality: Barn Bluff, 1559 m, Tasmania, 41°44'S., 145°55'E.

Collector: F. J. Mitchell.

Date of collection: January 16, 1963.

Description: As for holotype except as follows. Mature adults: Snout-vent length 50.0-67.0 mm, mean 58.8 (13 specimens); Intact tail 120-132% (mean 126.7%) of S-V length (3 specimens); Total length of adults with intact tails 114.0-128.0 mm, mean 119.3 mm (3

specimens); Length of forelimb 15-22 mm, mean 17.4 mm, 25-38% (mean 29.3%) of S-V length (13 specimens); Length of hindlimb 20-25 mm, mean 22.4 mm, 35-46% (mean 37.8%) of S-V length (13 specimens). Half-grown specimens: Snout-vent length 40.0 and 32.0 mm; Intact tail 117 and 118% of S-V length; Total length 87.0 and 70.0 mm; Length of forelimb 12 and 11 mm, 30 and 34% of S-V length; Length of hindlimb 16 and 14 mm, 40 and 43% of S-V length (half-grown specimens QVM 1947.3.4. d-e respectively). Juvenile at birth: Snout-vent length 25.0 mm; Intact tail 32 mm, 128% of S-V length; Total length 57.0 mm; Length of forelimb 9 mm, 36% of S-V length; Length of hindlimb 12 mm, 48% of S-V length (NMV D 18249). Supranasals absent in all paratypes. Postnasals partially separated off in QVM 1947.3.4. e. Frontoparietals fused in all the paratypes. Interparietal separate, large, varies from about one third to one fifth the size of the frontoparietals. One very enlarged pair of nuchal scales in 15 of the paratypes, QVM 1947.3.4. a has no enlarged nuchals. Seven supraciliaries in 14 of the paratypes, NMV D 18248 and QVM 1947.3.4. c each have eight supraciliaries. Eight upper labials with sixth subocular in 13 of the paratypes, NMV D 18242, NMV D 18246 and QVM 1947.3.4. d have seven upper labials with the fifth subocular. Lamellae under the fourth toe 20-25, mean 22.7, mode 23. Midbody scales in 40-44 rows, mean 41.6, mode 42.

Colour of all sixteen paratypes as for holotype.

L. greeni can be easily separated from its closest relatives *L. pretiosa* and *L. ocellata* as follows:

1. Midbody scales in 30-39 rows, dorsal surface brown with scattered light and dark patches, black upper lateral surfaces with scattered light patches *L. pretiosa*
Midbody scales in 40 or more rows, colour not as above 2
2. Midbody scales in 45-58 rows, light grey to olive-grey dorsal surface with black mottling, brown upper lateral surface with large ocellations—light grey patches surrounded by black *L. ocellata*

Midbody scales in 40-44 rows, black dorsal and lateral surfaces—most scales with a small grey-green central patch . . . *L. greeni*

COMMENT

L. greeni is the only reptile species restricted to the Tasmanian mainland. It was originally thought to be closely related to *L. pretiosa*, but more critical examination has indicated that *L. ocellata* is its closest relative. *L. greeni* and *L. ocellata* are sympatric on the summit of Mt. Barrow and there is no trace of hybridization thus they are good biological species (*sensu* Mayr 1963).

The species is named in honour of Bob Green, Zoologist in the Queen Victoria Museum, Launceston, in recognition of his help in gathering the material presented here and also for his extensive work on the vertebrate fauna of N. and W. Tasmania and the Bass Strait area. His collections in the Queen Victoria Museum have helped many zoologists complete projects which required material from the more inaccessible parts of Tasmania and Bass Strait.

DISTRIBUTION

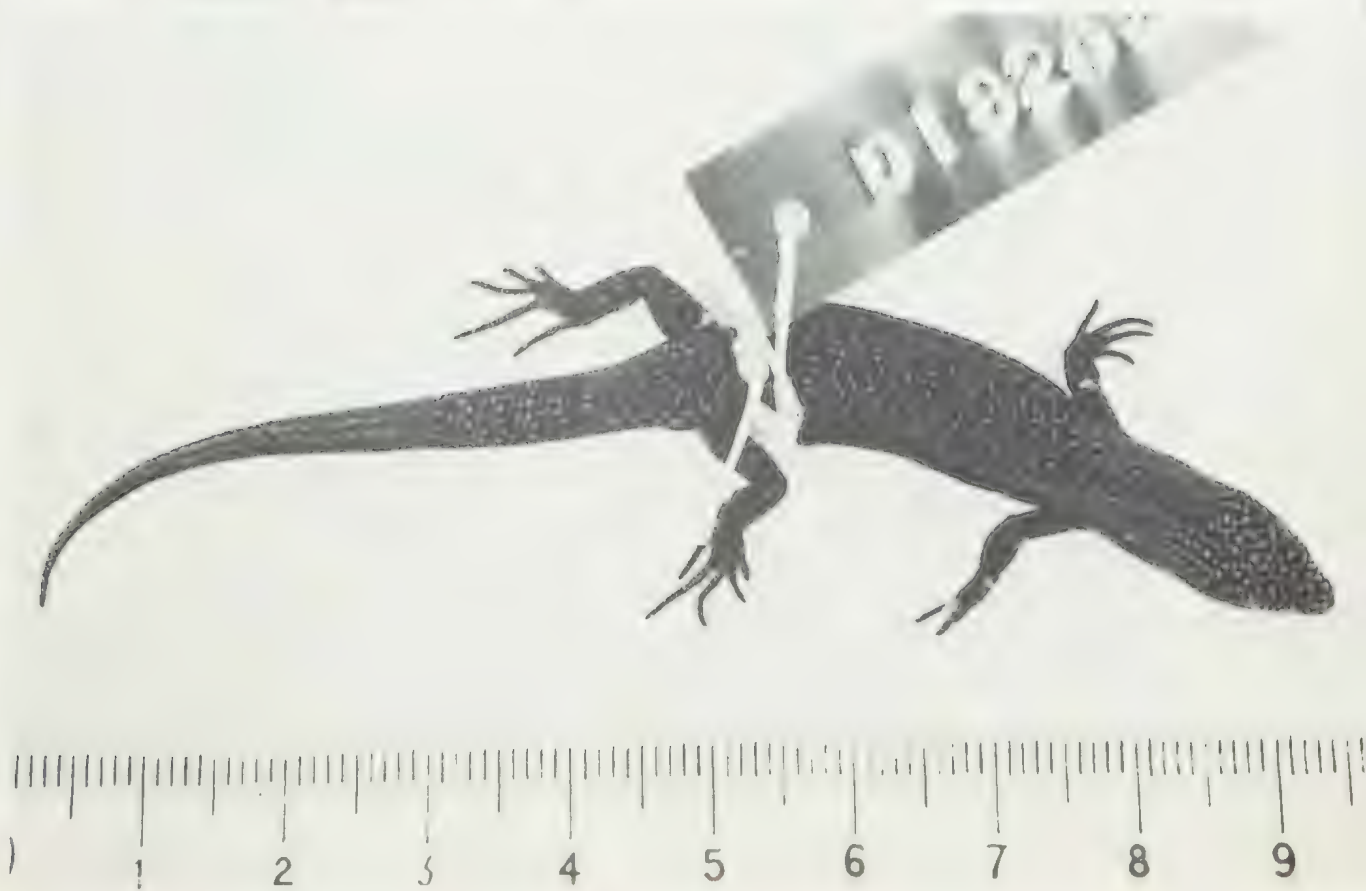
Found only on the Tasmanian mainland where it is restricted to alpine areas. Known from the Mount Barrow and Ben Lomond Massifs in the NE., and the Great Lake, Cradle Mountain and Lake St. Clair areas in the centre and NW. The species occurs disjunctly in a number of isolates within these areas.

HABITAT

All the known localities for this species are at altitudes over 1000 m in true alpine areas, i.e. above the tree line (Rawlinson 1974a,b). Precipitation in all the localities is high (more than 127 cm per year) and much of this falls as snow. Populations are restricted to the rocky banks of streams and swamps. The bare surfaces of rocks projecting from the stream or swamp banks are used for basking sites during activity and burrows under rocks in waterlogged soil along the banks are utilized for microenvironments during periods of inactivity. This is the only species of reptile in Australia which is restricted to alpine areas.



Fig. 1—Holotype of *Leiopisma coventryi* sp. nov.
NMV D40080 photographed in life.



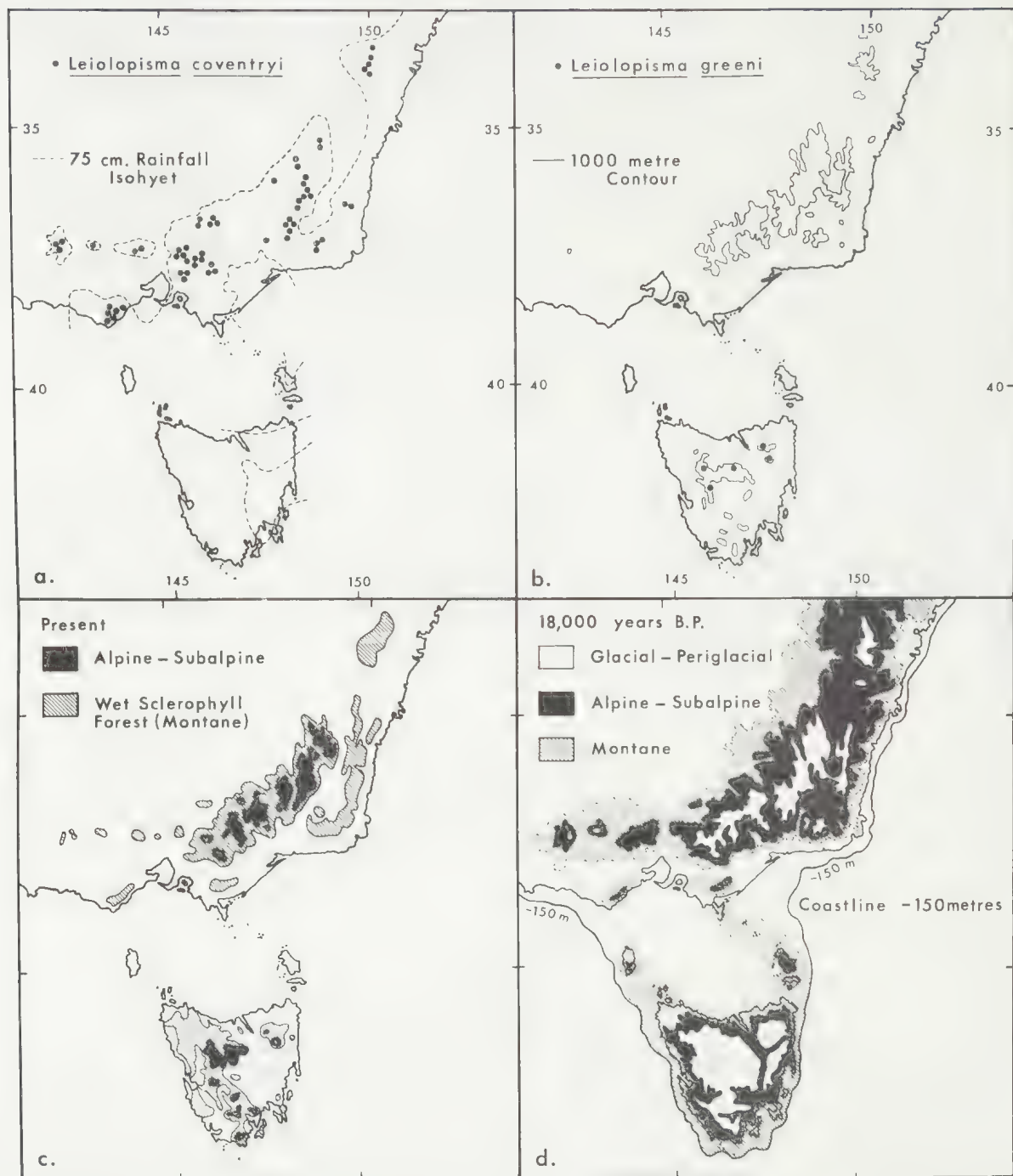


Fig. 3(a)—Distribution of *Leiolopisma coventryi* sp. nov. in SE. Australia and position of the 75 cm rainfall isohyet.

Fig. 3(b)—Distribution of *Leiolopisma greeni* sp. nov. in Tasmania and position of the 1,000 m contour.

Fig. 3(c)—Map of SE. Australia showing present

extent of the alpine and sub-alpine zones and the montane wet sclerophyll forest.
Fig. 3(d)—Map of SE. Australia showing approximate extent of the glacial and periglacial zones; the alpine and sub-alpine zones; the montane zone; and coastline (-150 m contour) 18,000 y. B.P. during the Late Wisconsin glacial phase.

ECOLOGY

L. greeni is an insectivorous skink with a thermoregulatory pattern during activity that classifies it as a shuttling heliotherm (Rawlinson 1974 a,b,c). The exposed rock surfaces are used for basking sites and foraging takes place on the rock surfaces and through the low alpine vegetation. When inactive, burrows under rocks in waterlogged soil along the stream or swamp banks are used and it is assumed these form the hibernation sites also. If pursued, *L. greeni* will not hesitate to escape by diving under submerged rocks in streams, even though the water temperature may be as low as 5°C.

Laboratory measurements of the thermal preferences and "Normal Activity Range" of *L. greeni* have been made from continuous recordings of body temperature in a photo-thermal gradient (see above). The results are summarized in Table 2. As with *L. coventryi*, specimens in the gradient mirrored their "shuttling" method of thermoregulation in the field. From measurements of body temperature made at one minute intervals on 6 specimens (1009 observations) it was determined that the "Mean Preferred" body temperature was 28.9°C., while the "Voluntary Minimum" and "Voluntary Maximum" body temperatures were 21.5°C. and 37.3°C. respectively (Table 2). The histogram of frequency of body temperatures maintained during activity (1°C. class intervals, range 19°-37°C.) is skewed slightly towards the high temperature end of the scale. The mode is the 29°C. class interval which contains only 13% of the observations. This result reflects the shuttling method of thermoregulation as discussed above for *L. coventryi*.

The physiological thermal tolerances of the species are unknown as no values have yet been obtained for the "Critical Maximum" or "Critical Minimum" body temperatures. *L. greeni* tolerates relatively wide fluctuations in body temperature during normal activity, the mean activity range for specimens was 15.8°C. (21.5°-37.3°C.) and the absolute range was 18.6°C. (19.0°-37.6°C.). These ranges are close to those of *L. coventryi* (see above) and *P. spenceri* (Rawlinson 1974c), both of which

also occupy low temperature habitats, thus wide voluntary thermal tolerances are probably an essential requirement for cold temperate reptiles.

REPRODUCTION

L. greeni is a live-bearing skink. There is no trace of eggshells around developing embryos, so it is assumed the species is fully viviparous (i.e. placental). Pregnant females kept under observation in the laboratory produced litters on March 10. Only three pregnant females were examined, litter size in each was 3, thus the mean number of offspring was also 3.0 (Table 2).

RELATIONSHIPS OF *LEIOLOPISMA GREENI*

The palatal bone structure shows that *L. greeni* (like *L. coventryi* sp. nov.) is an "alpha" *Leiolopisma* species. *L. greeni* has 40-44 mid-body scale rows, thus unlike *L. coventryi*, it belongs in the second group of "alpha" *Leiolopisma* species, viz. species with high midbody scale counts (see above) and its closest relatives are undoubtedly *L. ocellata* and *L. pretiosa*. It is considered that *L. greeni* is a sibling species of *L. ocellata*. The partially separated supranasals in the holotype and partially separated postnasals in one of the paratypes suggest that this species may have closer affinities with the genus *Pseudemoia* than was realized in the past (see also Rawlinson 1974c).

Biogeography

L. coventryi and *L. greeni* belong to the "alpha" *Leiolopisma* group of skinks which has radiated widely in the S. Pacific cool temperate area during the Quaternary. Both species have unusual distribution patterns and the explanations of these lie in the climatic and sealevel changes of the Late Wisconsin glacial phase and the post-glacial phase (Rawlinson 1974a, b,c). The Late Wisconsin lasted from 40,000-10,000 y. B.P. and it was either the most intense or one of the most intense Quaternary glaciations in SE. Australia (Galloway *et al.* 1973). A full account of the environmental changes has been given elsewhere (Rawlinson 1974a,b), but a summary of the main points plus some further information is given below

TABLE 2

Thermal tolerances and reproduction of *Leiolopisma greeni* sp. nov.

Body Temperature Value/Litter Size	Number of Observations	Mean	Range
<i>Thermal tolerances:</i>			
Critical Minimum Temperature °C.	—	—	—
Voluntary Minimum Temperature °C.	6	21.5	19.0-25.0
Mean Preferred Temperature °C.	1009	28.9	—
Voluntary Maximum Temperature °C.	6	37.3	36.9-37.6
Critical Maximum Temperature °C.	—	—	—
<i>Reproduction:</i>			
Litter Size	3	3.0	3-3

in order to discuss the distribution patterns of *L. coventryi* and *L. greeni* more fully.

Sealevel started to fall as water was locked up in glacial ice about 35,000 y. B.P., and it reached minus 80 m about 22,500 y. B.P. connecting Tasmania to Australia by a landbridge, the "Bassian Isthmus". Sealevel continued to fall until about 20,000-18,000 y. B.P. when the sea lay at minus 132-150 m. After 18,000 y. B.P., a rapid rise in sealevel commenced (the "Flandrian Transgression") as the glacial ice started to melt and by 12,750 y. B.P. it had reached minus 80 m breaking the Bassian Isthmus and isolating Tasmania (and the Bass Strait islands) from Australia. This rapid rise continued until 6,000 y. B.P. and the present coastline was attained at about 5,000 y. B.P. Thus Tasmania was connected to Australia for about 9,750 years (22,500-12,750 y. B.P.) while S. Australia was being subjected to the full glacial climate.

During the glacial phase mean air temperatures were lowered by about 5°C. at sealevel and up to 11°C. at the higher altitudes (above 2,000 m). The westerly wind system continued to influence SE. Australia, but there apparently was an increase in the south-westerly (snow bearing) winds and a decrease in the north-westerly (rain bearing) winds. Precipitation changed drastically during and after the glacial phase; after Bowler (1970) and Bowler and

Hamada (1971) the sequence seems to be as follows:

- Pre 30,000 y. B.P., low effective precipitation.
- 30,000-18,000 y. B.P., medium effective precipitation.
- 18,000-10,000 y. B.P., very low effective precipitation, arid period.
- 10,000-5,500 y. B.P., very high effective precipitation, pluvial period.
- 5,500-Present, medium effective precipitation.

Thus at the time the Bassian Isthmus broke up 12,750 y. B.P., SE. Australia was experiencing a very cold and very dry climate.

The altitudinal stratification of mountain zones was also severely depressed during the glacial phase. It is possible to recognize five mountain zones in SE. Australia:

1. Glacial zone: above the permanent snow-line, ice covers the ground all year, no vegetation.
2. Periglacial zone: ground freezes in winter and thaws in summer, no permanent vegetation.
3. Alpine zone: above the tree-line, ground continuously covered with snow for more than four months each year, vegetation low and stunted.

4. Sub-alpine zone: above the permanent winter snow-line and below the tree-line, ground continuously covered with snow for 1-4 months each year, vegetation woodland dominated by cold tolerant trees such as *Eucalyptus pauciflora* or *E. coccifera*.
5. Montane zone: below the permanent winter snow-line, snow lies on ground for short periods only, vegetation variable, if precipitation is high enough wet sclerophyll forest (dominated by large eucalypts such as *E. delegatensis*, *E. nitens* or *E. regnans*) or temperate rainforest (dominated by *Nothofagus cunninghami*) develops.

After studies published by several workers (Costin 1954, 1957, 1959, 1971; Davies 1967; Derbyshire 1972; Galloway 1965; Galloway *et al.* 1973; Jackson 1965; Peterson 1971) it is possible to estimate the lower limits of each of these zones once the altitude of an easily recognized marker such as the tree-line has been established. If the tree-line lies at X metres, then the lower limits of the various zones can be calculated as follows:

1. Glacial zone: (depends on temperature and snowfall) = $X + (200-1,000 \text{ m})$.
2. Periglacial zone: (depends only on temperature) = $X + 100 \text{ m}$.
3. Alpine zone: (depends only on temperature) = $X \text{ m}$.

4. Subalpine zone: (depends only on temperature) = $X - 300 \text{ m}$.
5. Montane zone: (depends on temperature and rainfall) = $X - 900 \text{ m}$.

Estimates are available for the altitudes of these zones in SE. Australia and Tasmania at present and during the Late Wisconsin glacial phase 20,000-18,000 y. B.P. (see Rawlinson 1974a,b; plus authors listed above). These estimates are summarized in Table 3 and Pl. 2., figs. 3c and 3d. As *L. coventryi* is restricted to montane wet sclerophyll forest and *L. greeni* is restricted to the alpine zone, the present distribution patterns need to be explained in the light of the changes outlined above.

L. coventryi has previously been designated as a post-glacial intrusive into S. Victoria (Rawlinson 1971, 1974a,b, as *L. weekesae*?). The species has a disjunct distribution in the montane wet sclerophyll forests of SE. Australia, but is absent from this vegetation form in Tasmania although wet sclerophyll forest is extensive there. These forests grow in areas of high rainfall (greater than 75 cm per year) in the montane zone. During the Late Wisconsin, the montane zone descended to sealevel (i.e. the low glacial sealevel of minus 132-150 m) in the Bass Strait area and Tasmania, thus there was a much more extensive montane area available which would be expected to

TABLE 3
Mountain zones in SE. Australia.

Area and Period	Altitude of lower limit in metres relative to present sea level				
	Glacial Zone	Periglacial Zone	Alpine Zone	Sub-alpine Zone	Montane Zone
<i>Tasmania:</i>					
Present 0 y. B.P.	—	1300	1200	900	300
Late Wisconsin, 18,000 y. B.P.	600-1350	450	350	50	-550*
<i>S. Victoria:</i>					
Present 0 y. B.P.	—	1850	1750	1450	850
Late Wisconsin, 18,000 y. B.P.	—	900	800	500	-100*
<i>SE. N.S.W. and A.C.T.:</i>					
Present 0 y. B.P.	—	1950	1850	1550	950
Late Wisconsin, 18,000 y. B.P.	1850-2050	1000	900	600	0

* Sea level lay at minus 132-150 m 18,000 y. B.P.

facilitate the movement of *L. coventryi* southward. However, the species did not reach Tasmania (or any Bass Strait islands) so it is reasonable to conclude that the vegetation form inhabited (wet sclerophyll forests) was very restricted and this is consistent with the theory that precipitation was greatly reduced during the glacial phase. The species probably expanded its range into S. Victoria as wet sclerophyll forests expanded during the post-glacial period 10,000-5,500 y. B.P. after the Bassian Isthmus was broken up (12,750 y. B.P.). Subsequently the climate has become more arid (after 5,500 y. B.P.) resulting in the present disjunction of the species. Thus the distribution of this species supports the theory that the Late Wisconsin glacial phase was a period of aridity and there was a post-glacial pluvial period.

L. greeni has previously been designated as a Tasmanian glacial relict (Rawlinson 1971 as *L. pretiosum* Form B and Rawlinson 1974b,c, as *Leiopisma* sp. nov.). The species has a disjunct distribution in the alpine areas of the NE. and the Central Plateau. Alpine areas are now largely restricted to altitudes above 1,200 m, however during the Late Wisconsin the lower limit descended to 350 m (Table 3, Pl. 2., fig. 3d), thus the alpine area was much greater than at present and the distribution of *L. greeni* would have been much more extensive than at present. However, even if it had occupied all available alpine areas, the species would not have reached the Bass Strait islands or S. Victoria for the low elevation of the Bassian Isthmus would have prevented the formation of alpine vegetation in all but a few localities. As the glacial phase receded, the alpine zone retreated to its present level fragmenting the range of *L. greeni* and leaving the species in its present disjunct high altitude localities. Thus the distribution of this species supports the theory that the alpine zone was much more extensive in Tasmania during the Late Wisconsin glacial phase.

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The author thanks Dr H. G. Cogger of the Australian Museum, Mr A. J. Coventry of

the National Museum of Victoria, Dr T. F. Houston of the South Australian Museum and Mr R. H. Green of the Queen Victoria Museum for help in locating specimens in the collections under their care. Mr J. McNally, Director of the National Museum of Victoria, kindly allowed the facilities of the Museum to be used during work on the species descriptions.

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NOTES ON ADDITIONS, CHANGES AND THE DISTRIBUTION OF THE AUSTRALIAN WATER-BUG FAUNA (HEMIPTERA-HETEROPTERA)

By I. LANSBURY

Hope Department of Entomology, University Museum, Oxford

Introduction

By the courtesy of Mr A. Neboiss, National Museum of Victoria, Melbourne; Dr T. E. Woodward, University of Queensland; Dr T. Weir, Department of Northern Territory, Darwin; Dr I. A. E. Bayly, Monash University and Miss J. Knowles of Monash University, I have been able to study several collections of aquatic Heteroptera from various localities, principally Victoria, with smaller collections from Queensland, Fraser Island, Q., Northern Territory and Tasmania. Noteworthy is the discovery of a striking new species of *Anisops* (Notonectidae) from Northern Queensland and the confirmation of the discovery of *Cercotmetus* (Nepidae) new to the Australian fauna with a new subspecies of *brevipes* Montandon from Northern Queensland and the Northern Territory.

I wish to thank Dr A. S. Menke, United States National Museum, Washington for providing a figure of the Holotype of a little known species, *Anisops malkini* Brooks from Northern Australia. Finally, I wish to thank Dr G. Gross, South Australian Museum, Adelaide for the loan of a series of *Sigara* (*Tropocorixa*) *australis* (Fieber) which enabled me to solve an extremely puzzling problem which is dealt with in detail in these notes.

Nepidae

Ranatra diminuta Montandon: Queensland, Fraser Island, Coomboo Lake, 5.i.1972, I. A. E. Bayly (I.A.E.B.) 2 ♀, 5 immature. F.I., Boomerang North, 10.i.1972, I.A.E.B., immature specimens. F.I., Hidden Lake, 8.i.1972, I.A.E.B., immature specimens. F.I., Deep Lake, 10.i.1972, I.A.E.B., immature specimens.

Laccotrephes tristis Stal: Queensland, Fraser Island, Coomboo Lake, 5.i.1972, I.A.E.B., 1 ♂. F.I., Wabby Lake, I.A.E.B., immature specimen. F.I., Lake Bowarrady, 7.i.1972, I.A.E.B., 1 ♀.

Cercotmetus brevipes australis subsp. n.

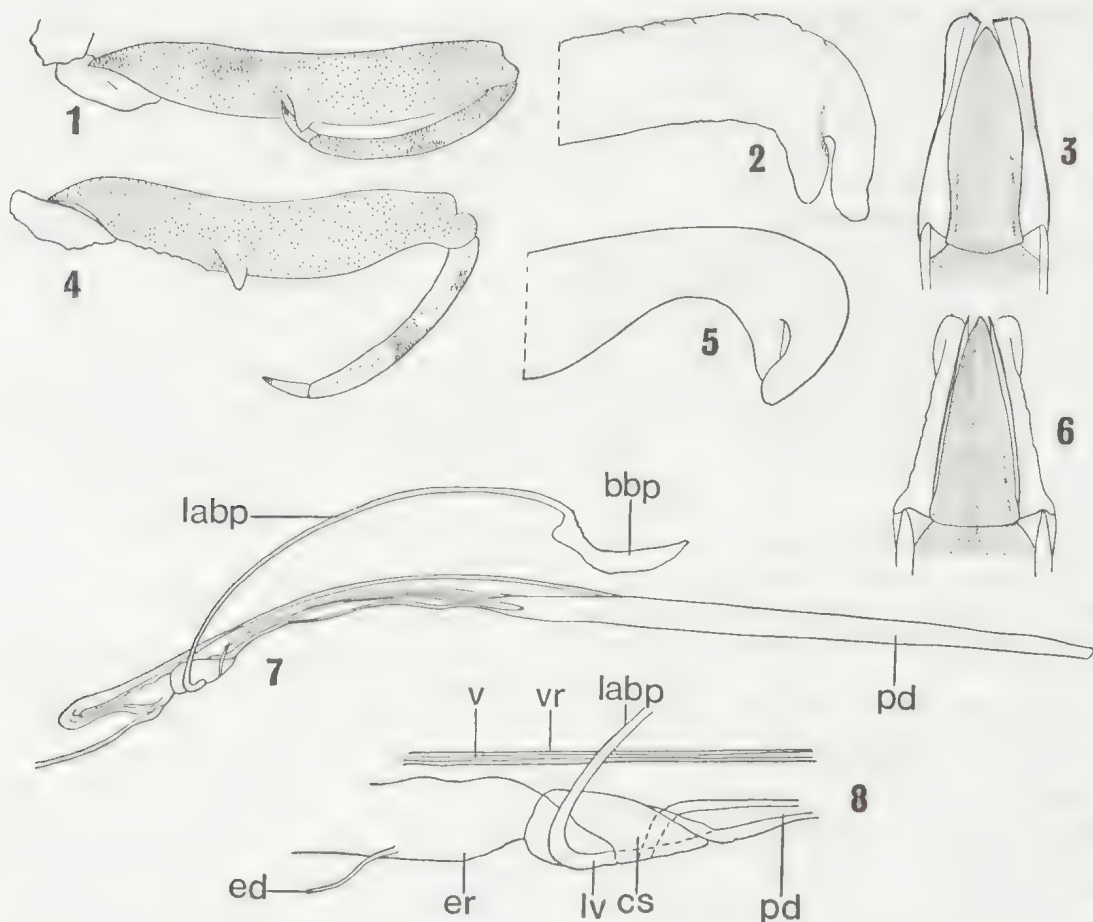
(Figs. 1-3, 7 and 8)

Males, 36.5 mm long, respiratory siphon 8 mm long, ♀ 38 mm long, respiratory siphon 8.5 mm long.

General appearance similar to nominate form, differs in features as tabulated below:

<i>brevipes australis</i> subsp. n.	<i>brevipes brevipes</i> Montandon
Front femora not noticeably sinuate or deeply concave posteriorly (Fig. 1)	Front femora sinuate, deeply concave posteriorly (Fig. 4)
Front tibiae with two clear yellowish bands (Fig. 1)	Front tibiae mostly pale yellow (Fig. 4)
Middle femora slightly longer than median length of pronotum	Middle femora shorter than median length of pronotum
Hind femora reaching posterior margin of 5th sternite	Hind femora not reaching posterior margin of 5th sternite
Male operculum not triangular (Fig. 3)	Male operculum triangular (Fig. 6)

Male genitalia (Figs. 2, 7 and 8) typical of genus *Cercotmetus*. The bridge, basal plates and lateral arms are very long and lightly sclerotised. Lamina ventralis vestigial. Central strut large and almost hyaline. Ejaculatory reservoir elongate. Vesica partially enclosed within a rod which is quite heavily sclerotised anteriorly becoming rather more membranous distally. Posterior diverticulum simple, rather more sclerotised than the median phallosome. Paramere (Fig. 2) similar to nominate form. Specimens of *brevipes brevipes* from Viet-Nam have slightly different parameres (Fig. 5) but do not differ in any other way from nominate form. Figure 5 is drawn from a dry mounted specimen whereas figure 2 is of a specimen which has been cleared in KOH and passed through glacial acetic acid, etc.



Figs. 1-3, 7 and 8 *Cercotmetus brevipes australis* subsp. n. ♂: 1, front leg. 2, paramere. 3, operculum. 7, internal genitalia: bbp bridge and basal plates; cs central strut; ed ejaculatory duct; er ejaculatory reservoir; labp lateral arms of the basal plates; lv lamina ventralis; pd posterior diverticulum; v vesica; vr vesical rod. 8, detailed view of central strut and associated structures. Figs. 4-6 *Cercotmetus brevipes brevipes* Montandon ♂: 4, front leg. 5, paramere. 6, operculum.

Holotype ♂, Australia, Northern Territory, 12°16' S-133°13' E, Birraduk Creek, 16 km W. by SW. of Nimbuwah Rock, 4.vi.1973, T. Weir in the collection of the Department of Northern Territory, Darwin.

Paratypes: 1 ♂, Northern Territory, 12°06' S-133°04' E, Cooper Creek, 19 km E. by S. of Mt. Borrodaile, 5.vi.1973, T. Weir, Oxford.

1 ♂, Northern Territory, Berry Springs, 64 km south of Darwin, 28.x.1970, T. Weir, Queensland University Collection.

In addition to the three adults listed, the following immature specimens of *brevipes australis* have been examined:

Two immature: Northern Territory, 12°17' S-133°20' E, Cooper Creek, 11 km S. by W. of Nimbuwah Rock, 3.vi.1973, T. Weir, Department of Northern Territory, Darwin. One immature: North Queensland, Hann River, 80 km north of Laura, 26.x.1969, B. Cantrell, Queensland University Collection.

In a footnote Lansbury (1973) refers to an immature *Cercotmetus* from Australia, Groote Eyland, 5.vi.1948, R. R. Miller as being either a new species or *dissidens* Montandon so far only known from New Guinea. It is thought likely that this specimen may be referable to *brevipes australis*. The nominate form has a very wide distribution: Sumatra, Java, Sarawak, India (Bengal), Thailand, Viet-Nam, Philippines and China (Fukien). Lansbury (1973)

synonymised *C. formosanus* Sonan from Formosa with *brevipes*.

In Lansbury (1973) *brevipes australis* does not key correctly, the key should be amended as follows:

- 2 (1) Not more than 42 mm long 2A
 – More than 47 mm long 3
 2A (2) Middle femora clearly shorter than the median length of the pronotum, front femora sinuate . . . *brevipes brevipes* Montandon.
 – Middle femora longer than the median length of the pronotum, front femora not noticeably sinuate . . . *brevipes australis* subsp. n.

Notonectidae

Anisops nasuta Fieber: Queensland, Fraser Island, Boomerang South, 9.i.1972, I.A.E.B., 1 ♀, F.I., Basin Lake, I.A.E.B., 1 ♂, 15 ♀ 1 immature.

Anisops elstoni Brooks: Queensland, Fraser Island, AB Lake, 10.i.1972, I.A.E.B. 4 ♂, 8 ♀.

Anisops gratus Hale: Victoria, Dam 25 km before Warrambine Creek, Hamilton road from Geelong, 23.iv.1971, J. Knowles (J.K.) 2 ♂.

Anisops deanei Brooks: Victoria, Jaractnear Lake, 5.ix.1971, -Hang, 1 ♂. Queensland, Creek on Esk road near Ipswich Junction, 22.v.1971, J.K., 1 ♂.

Anisops evansi Brooks: Victoria, Lake Struan, 26.vi.1971, J.K., 8 ♂, 7 ♀. Not previously recorded from the mainland of Australia and thought to be a Tasmanian endemic.

Anisops barrensis Brooks: Queensland, Creek on Esk road near Ipswich Junction, 22.v.1971, J.K., 1 ♂. This specimen does not agree in some important details with paratypes of *barrensis*.

Anisops thienemanni Lundblad: New South Wales, Lagoon next to Lake Victoria, 8.iv.1971, J.K.; 8 ♂, 9 ♀. Victoria, Dam 25 km before Warrambine Creek, Hamilton road from Geelong, 23.iv.1971, J.K., 2 ♂, 2 ♀. Little Lake next to Dam 25 km before Warrambine Creek, Hamilton road from Geelong, 25.iv.1971, J.K., 6 ♂, 2 ♀. Dam near Lake Murdeduke, 26.vi.1971, J.K., 4 ♀. Lake Purrumbete, Camperdown, 25.iv.1971, J.K., 7 ♂, 1 ♀. Victoria,

Jaractnear Lake, 5.ix.1971, -Hang, 2 ♂, 3 ♀. Tchem Lake, 20.iii.1971, -Hang, 2 ♂, 6 ♀. Streatham "Blythvale" Billabong, 24.iv.1971, J.K., 1 ♂, 1 ♀. Streatham "Blythvale" river behind house, 24.iv.1971, J.K., 2 ♂, 2 ♀. Lake Coleman, 19.vi.1971, B. Chessman, 3 ♂, 7 ♀. Lake Struan, 26.vi.1971, J.K., 1 ♂, 1 ♀.

Anisops planifacies sp. n.

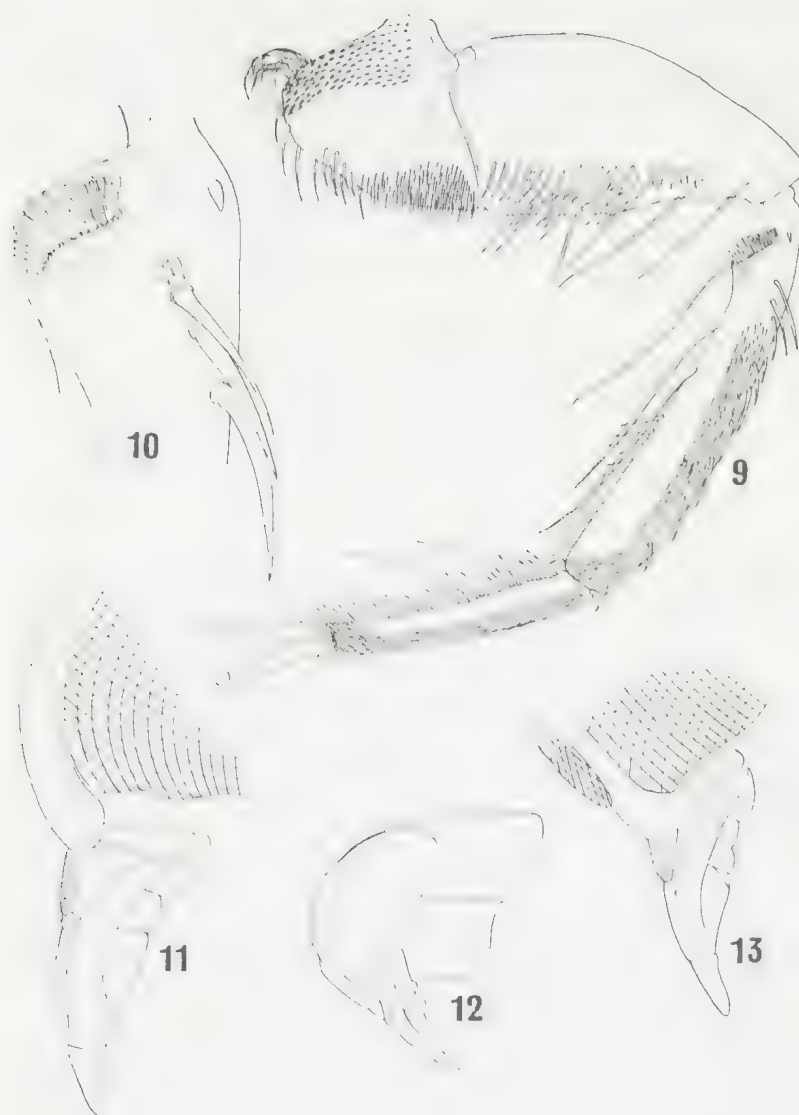
(Figs. 9-12)

Male 8.3 mm long, maximum width 2.5 mm, ♀ 8.9 mm long, maximum width 2.75 mm. Colour and structure ♂: Eyes dark brown. Pronotum, scutellum and most of the abdomen pale yellowish. Elytra hyaline. Posterior tergites and sternites black. Epimeron reddish brown.

Viewed from above, the anterior margin of the head is straight. Greatest width of head three-fourths pronotal humeral width and six times the anterior width of the vertex. Synthipsis just over half the anterior width of the vertex. Median head length two-thirds the median pronotal length. Pronotal humeral width twice the median length, lateral margins diverging and half the median length, posterior margin broadly emarginate. Facial tubercle raised between the lower margins of the eyes forming a flat platform (Fig. 11) not visible when viewed from above. Labrum basally broader than long and rather hairy. Rostral prong large. Stridulatory comb (Fig. 10) chaetotaxy of the male front leg (Fig. 9).

Female: Eyes black, posterior margin of the pronotum and scutellum orange. Tergites black with orange bands posteriorly. Underside entirely black. Viewed from above the head is more rounded than in the male. Greatest width of head almost equalling pronotal humeral width and five and a half times the anterior width of the vertex. Median head length over half but less than two-thirds median pronotal length.

Comparative notes: This species keys out to couplet 16 (*malkini* Brooks and *occipitalis* Breddin) in Lansbury (1969). It can be distinguished from these two and all other Australian species by the raised facial tubercle. Brooks (1951) states that the frons of *malkini*



Figs. 9-12 *Anisops planifacies* sp. n. ♂: 9, front leg. 10, stridulatory comb. 11, oblique view of rostrum and rostral prong. 12, side view of head and pronotum. Fig. 13 *Anisops malkini* Brooks Holotype ♂: oblique view of rostrum and rostral prong.

are depressed and apically terminated by a transverse ridge. Dr Menke provided me with a sketch of the rostral prong and associated area of the Holotype of *malkini* described from a single male from Darwin (Fig. 13). It does not seem to be as Brooks described it, but does closely resemble *malkini* Brooks sensu Lansbury (1969) the description being based on a single male from Ord River, Western Australia. The chaetotaxy of the male front legs are all rather similar except that the male from the Ord River has four prominent spines on the

inner surface of the front tarsi which are lacking in the Holotypes of *malkini* and *planifacies*. Finally *malkini* from Darwin is 6.9 mm long compared with 7.5 mm from Western Australia, *planifacies* is much larger.

Holotype ♂ (T-4569) and allotype ♀ (T-4570), Australia, North Queensland, Hann River, 112 km south of Coen, 27.vi.1970, J. C. le Souef in the National Museum of Victoria, Melbourne.

Enithares woodwardi Lansbury: Queensland, Fraser Island, Boomerang South, 9.i.1972,

I.A.E.B., 1 ♀, 1 immature. F.I., AB Lake, 10.i.1972, I.A.E.B., 1 ♂, 1 ♀. Creek on Esk road near Ipswich Junction, 22.v.1971, J.K., 1 ♂. Victoria, Little Lake next to Dam 25 km before Warrambine Creek, Hamilton road from Geelong, 25.iv.1971, J.K., 2 ♂, 3 ♀. Home Station Creek, Delatite, 25.viii.1971, H. B. Hynes, 1 ♂, 5 ♀. Streatham, "Blythvale" Billabong, 24.iv.1971, J.K., 1 ♂, 1 ♀. Streatham, "Blythvale" river behind house, 24.iv.1971, J.K., 1 ♂.

Enithares hackeri Hungerford: Queensland, Creek on Esk road near Ipswich Junction, 22.v.1971, J.K., 4 ♂, 3 ♀. This species is now known to occur in New Guinea (Lansbury, in press), 1 ♂, 2 ♀ have been studied from Madang District, Finisterre Mts., Moro 5,500' St. 7, 30.x.-15.xi.1964, M. E. Bacchus (British Museum, Natural-History).

Corixidae

Agraptocorixa hirtifrons (Hale): Victoria, Dam 25 km before Warrambine Creek, Hamilton road from Geelong, 23.iv.1971, J.K., 1 ♂. Lake Coragulac, Alvie, 25.iv.1971, J.K., 1 ♀. Lake Linlithgow, 24.x.1971, B. Chessman, 2 ♀. Lake Muirhead, 24.x.1971, B. Chessman, 1 ♀. *Agraptocorixa parvipunctata* (Hale): New South Wales, Lagoon next to Lake Victoria, 8.iv.1971, J.K., 2 ♂, 4 ♀. Victoria, Dam 25 km before Warrambine Creek, Hamilton road from Geelong, 23.iv.1971, J.K., 1 ♀. Little Lake next to Dam 25 km before Warrambine Creek, Hamilton road from Geelong, 25.iv.1971, J.K., 1 ♂. Lake Muirhead, 24.x.1971, B. Chessman, 2 ♀.

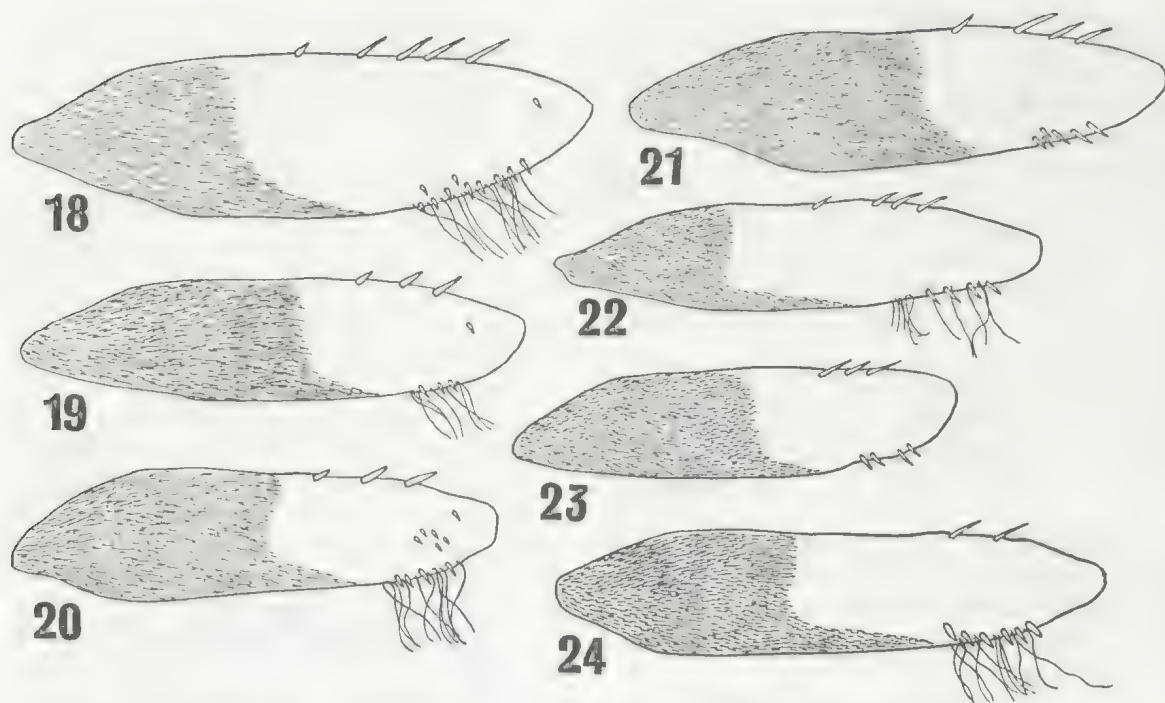
Agraptocorixa eurynome (Kirkaldy): New South Wales, Lagoon next to Lake Victoria, 8.iv.1971, J.K., 1 ♀. Victoria, Little Lake next to Dam 25 km before Warrambine Creek, Hamilton road from Geelong, 25.iv.1971, J.K., 1 ♂, 1 ♀. Dam near Lake Murdeduke, 26.vi.1971, J.K., 5 ♂. Lake Purrumbete Camperdown, 25.iv.1971, J.K., 1 ♂. Tchem Lake, 20.viii.1971, -Hang, 6 ♂, 6 ♀. Streatham, "Blythvale" river behind house, 24.iv.1971, J.K., 2 ♂, 4 ♀ and 8 immature. Lake Coleman, 19.vi.1971, B. Chessman, 1 ♀. Lake Clarke, 23.x.1971, B. Chessman, 1 ♂. Lake Muirhead,



Figs. 14-17 *Sigara (Tropocorixa) australis* (Fieber) ♂, Adelaide: 14-16 tergites 6-8, 17, "strigil".

24.x.1971, B. Chessman, 4 ♀. Streatham, "Blythvale" Billabong, 24.iv.1971, J.K., 1 ♀. *Sigara (Tropocorixa) truncatipala* (Hale): New South Wales, Lagoon next to Lake Victoria, 8.iv.1971, J.K., 1 ♂. Queensland, Creek on Esk road near Ipswich Junction, 22.v.1971, J.K., 2 ♂.

Sigara (Tropocorixa) sublaevifrons (Hale): New South Wales, Lagoon next to Lake Victoria, 8.iv.1971, J.K., 1 ♂. Victoria, Dam 25 km before Warrambine Creek, Hamilton road from Geelong, 23.iv.1971, J.K., 1 ♂. Little Lake next to Dam 25 km before Warrambine Creek, Hamilton road from Geelong, 25.iv.1971, J.K., 1 ♂, 1 ♀. Streatham, small Dam at "Blythvale", 24.iv.1971, J.K., 1 ♂, 1 ♀. Streatham, "Blythvale" river behind house, 24.iv.1971, J.K., 2 ♂, 11 ♀. Streatham, "Blythvale" Billabong, 24.iv.1971, J.K., 5 ♂, 21 ♀. Streatham, "Blythvale" water-tank Nixon,



Figs. 18-24 *Sigara* hind femora: 18, *australis* (Fieber). 19, *sublaevifrons* (Hale). 20, *truncatipala* (Hale). 21, *mullaka* Lansbury. 22, *tasmaniae* (Jaczewski). 23, *tadeuszi* (Lundblad). 24, *neboissi* Lansbury.

25.iv.1971, J.K., 1 ♂. Lake Purumbete, Camperdown, 25.iv.1971, J.K., 2 ♀. Lake Muirhead, 24.x.1971, B. Chessman, 1 ♂, 1 ♀.

Sigara (Tropocorixa) tasmaniae (Jaczewski): South West Tasmania, Lake Pedder, 10.iii.1972, A. Neboiss, 3 ♂, 8 ♀ and 1 immature. Tasmanian endemic, previous records, Tas. National Park, 1,066 m (Type locality) and Shannon Lagoon.

Sigara (Tropocorixa) neboissi Lansbury: North West Tasmania, Hellyer River Gorge, 9.ii.1971, A. Neboiss, 4 ♀. Tasmanian endemic, previous records, Shannon Lagoon; Hobart; Lake Tiberias and Ridgeway. This species is rather like *truncatipala* (Hale) which is widespread in South Australia, Victoria, New South Wales and parts of Queensland.

Sigara (Tropocorixa) australis (Fieber): Victoria, Lake Struan, 26.vi.1971, J.K., 13 ♂. Lake Linlithgow, 24.v.1971, B. Chessman, 19 ♂, 3 ♀. Lake Coleman, 19.vi.1971, B. Chessman, 7 ♂, 5 ♀. Lake Clarke, 23.x.1971,

B. Chessman, 1 ♂, 6 ♀; not typical, much paler than usual, black pronotal markings very narrow. Streatham, "Blythvale" river behind house, 24.iv.1971, J.K., 1 ♀. Dam near Lake Murdeduke, 26.vi.1971, J.K., 1 ♂, 2 ♀. Lake Muirhead, 24.x.1971, B. Chessman, 1 ♂, 5 ♀. Lake Terangpom, 25.iv.1971, J.K., 7 ♂, 6 ♀. Lake Coragulac, Alvie, 25.iv.1971, J.K., 3 ♂, 6 ♀. Lake Purumbete, Camperdown, 25.iv.1971, J.K., 1 ♀. Lake Purdigulac, 17.v.1971, B. V. Timms, 4 ♂. Lake Rosine, 24.x.1971, B. Chessman, 2 ♂, 2 ♀. Gnarkeet Creek near Foxhow, 16.iv.1971, B. Chessman, 1 ♂, 1 ♀. Lake Colac, 13.iv.-18.vi.1971, B. V. Timms, 10 ♂, 10 ♀.

It can be inferred from the existing data that *australis* is characteristic of lakes and rivers and appears to be fairly common in Victoria. Lansbury (1970) figured the 8th tergite incorrectly, the three groups of hairs shown on this tergite were in fact groups which had become detached from the distal margin of the 7th tergite during the preparation of the slide. The correct appearance of the 6th-8th tergites are as shown in figures 14-16, the 'strigil' (Fig. 17). Specimens from Victoria, Lakes Muirhead; Terangpom; Coragulac; Clarke; Dam

near Lake Murdeduke; Struan; Linlithgow; Coleman as well as material from South Australia, Adelaide, reed beds and Murray Bridge have been dissected to confirm the chaetotaxy of the tergites, none were found which resembled my 1970 figure. An error has been found in the first couplet of the 1970 key, the second line of the first couplet should read "Right clasper of male spine-like distally (figs. 54 and 67)" not figs. 97 and 98 as printed. The pilose areas of the hind femora of the Australian *Sigara* are of some additional help in separating some of the seven species although they are of no taxonomic value in distinguishing females of *truncatipala* from *sublaevifrons* which are often found in the same habitat.

An amended key is given which is based on Lansbury (1970) which includes references to the 1970 figures, these are in square brackets to distinguish them from the figures included in this paper.

Revised key to the Australian *Sigara*

- 1 Right clasper of male not spine-like distally [Figs. 13, 28 and 41] 2
- Right clasper of male spine-like distally [Figs. 54 and 67] 4
- 2 (1) Pala elongate, 3x longer than broad [Fig. 12]. Pilose area of hind femora not reaching half way along upper margin (Fig. 18) . . . *australis* (Fieber)
- Pala shorter, never more than 2.75x longer than broad [Fig. 27] 3
- 3 (2) Distal pala pegs much longer than remainder [Fig. 27]. Pilose area of hind femora reaching more than half way

along upper margin (Fig. 21)

mullaka Lansbury

- Distal pala pegs not significantly longer than remainder [Fig. 40]. Pilose area of hind femora not reaching half way along upper margin (Fig. 22) *tasmaniae* (Jaczewski)
- 4 (1) Frontal impression or fovea obsolete [Figs. 45 and 46] *sublaevifrons* (Hale)
- Frontal impression or fovea clearly defined [Figs. 58, 71 and 88] 5
- 5 (4) At most 5.6 mm long, usually just over 5 mm *tadeuszi* (Lundblad)
- At least 5.9 mm long 6
- 6 (5) Distal pala margin concave, not produced along lower margin [Fig. 80]. Pilose area of hind femora reaching about half way along upper margin (Fig. 20) *truncatipala* (Hale)
- Distal pala margin not concave, clearly produced along lower margin [Figs. 97 and 98]. Pilose area of hind femora not reaching half way along upper margin (Fig. 24) *neboissi* Lansbury

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THE GENERA *OPHIDIUS* CANDÈZE AND *YALGANUS* GEN. NOV. (ELATERIDAE: COLEOPTERA)

By A. NEBOISS

Curator of Insects, National Museum of Victoria

Abstract

The genus *Ophidius* Candèze is redefined and *O. vericulatus* sp. n. described. A key to the four included species (*dracunculus* Candèze, *elegans* Candèze, *histrion* (Boisduval) and *vericulatus* sp. n.) is provided. A new genus *Yalganus* is erected to include *serricornis* (Candèze) transferred from *Ophidius*, and *hirticornis* (Carter) transferred from *Dicteniophorus* Candèze.

Introduction

Candèze (1863) erected the genus *Ophidius* to contain three species, two of which (*elegans* and *dracunculus*) he described as new, and the third, *histrion* (Boisduval, 1835) transferred from genus *Elater* Linne. These three species formed a closely related group to which three further species were added during later years—*brevicornis* Macleay (1872), *serricornis* Candèze (1878), and *macleayi* Candèze (1895).

The genus *Ophidius* is characterized by the vertically raised scutellum, all legs with four distinctly padded tarsi, distinct genital structures in both sexes, and the absence of the frontal carina on the head. The combination of the above features are not present in the three latter species which are now excluded from the genus.

Detailed locality and collecting data are given for the new species only. The collections from which specimens were examined are listed below, together with abbreviations used in the text.

- AM—Australian Museum, Sydney.
- ANIC—Australian National Insect Collection, Canberra.
- BM—British Museum (Natural History), London.
- CAS—Californian Academy of Sciences, San Francisco.
- DANSW—Department of Agriculture, N.S.W., Sydney.
- DEI—Deutsches Entomologisches Institut, Berlin.
- HU—Humboldt University, Berlin.

- IRScNB—Institut Royal des Sciences Naturelles de Belgique, Brussels.
- JGB—Private collection of Mr J. G. Brooks, Cairns.
- MACL—Macleay Museum, Sydney.
- MF—Museum G. Frey, München.
- NMV—National Museum of Victoria, Melbourne.
- NRS—Naturhistoriska Riksmuseet, Stockholm.
- QM—Queensland Museum, Brisbane.
- QU—Queensland University, Brisbane.
- SAM—South Australian Museum, Adelaide.

Genus *OPHIDIUS* Candèze

Ophidius Candèze, 1863: 203; Candèze, 1891: 180; Schwarz, 1907: 235, 238; Neboiss, 1956: 55.
Type species: *Ophidius elegans* Candèze (designated by Hyslop, 1921).

The length of specimens in the genus range from 12 to 25 mm. They are rather brightly and conspicuously coloured with orange-brown and black patterns. The distribution of the genus is restricted to the eastern New South Wales and Queensland.

Generic diagnosis: Head convex with more or less distinct, somewhat triangular median depression; anterior carina absent, mandibles robust, bluntly bicuspid; maxillary palp with terminal segment hatchet shaped, antennae short, barely reaching back to the posterior angles of the prothorax, seg. 1 large, robust, slightly curved; seg. 2 very short, rounded; seg. 3 similar to seg. 2, but slightly more elongated; seg. 4-10 elongately triangular, laterally flattened, becoming shorter distally; terminal segment slightly recessed near apex.

Pronotum as wide as the elytra, covered with

line pubescence; lateral carina entire, although occasionally inconspicuous anteriorly; posterior angles short, divergent, pointed apically; dorsal carina very close and parallel to the lateral carina. Scutellum appears as a vertical column with flat or slightly dome-shaped top.

Prosternal suture straight, slightly excavated anteriorly. Posterior margin of mesosternal groove high, abruptly depressed anteriorly. Legs short, tarsal segments 1-4 becoming shorter distally, with distinct rounded pads.

Key to species of genus *Ophidius*

1. — Elytra concolorous 2
 - Elytra with black and orange-brown pattern 3
2. — Apex of elytra rounded (Fig. 10) *elegans*
 - Apex of elytra terminates in acute bifid point (Fig. 11) *vericulatus*
3. — Elytra with pattern in form of lines *histrion*
 - Elytra with pattern in form of spots *dracunculus*

Ophidius elegans Candèze

Figs. 1, 4, 5, 10, 17. Plate 3, fig. 1.

Ophidius elegans Candèze, 1863: 204; Candèze, 1895: 51; Neboiss, 1956: 55.

The original description is based on specimens from the Bakewell collection and includes both sexes. According to the available information this collection was passed on to Fleutiaux, whose collection is now in the Museum d'Histoire Naturelle, Paris. It is not known to the present author if there are any specimens of *elegans* in that institution and whether the type is among them. Three specimens (♂ and 2 ♀) in the IRScNB collection, Brussels are each labelled "Victoria" and a printed label "Type". The description of the female states that the abdomen is entirely black, this is not so with the two females and their status as 'syntypes' is doubtful.

The type locality "Victoria" is somewhat misleading; the southernmost specimens have been recorded from Monaroo, in Southern New South Wales, but none from Victoria. It is likely that the locality refers to Mt. Victoria in the Blue Mountains, which would fit well within the range of distribution.

Head, antennae, median line of pronotum, posterior angles as well as scutellum, legs and most of the underside of the body black, other parts orange-brown. Median depression of the head slight to moderate, not sharply defined, somewhat triangular.

Antennae serrate, pronotum evenly elevated, with moderately dense punctation. The top of scutellum almost flat or slightly depressed in the middle, punctate, edges rounded. Elytra gradually curved, apices conjointly rounded.

Aedeagus with lateral lobes slender, apical hooks elongate, median lobe gradually tapering. In female the base of bursa copulatrix densely covered with long chitinous spines, basal enlarged section of accessory gland with two groups of short stout spines.

Length 16-23 mm, width 4-6 mm.

Type location: Unknown (probably Paris Museum); 1 ♂ 2 ♀ syntypes (?) IRScNB.

Type locality: "Victoria" (?) see comments above.

Specimens examined: (28) New South Wales—Monaroo, Nowra (Jan.), Appin (Dec.), Sydney, Ropes Creek, National Park (Jan.), Galston, Wahroonga, Yanderra (Dec.), Queensland—Stanthorpe (Jan.). (ANIC; CAS; HU; IRScNB; JGB; NMV; QM; SAM).

Distribution: New South Wales, Sth. Queensland.

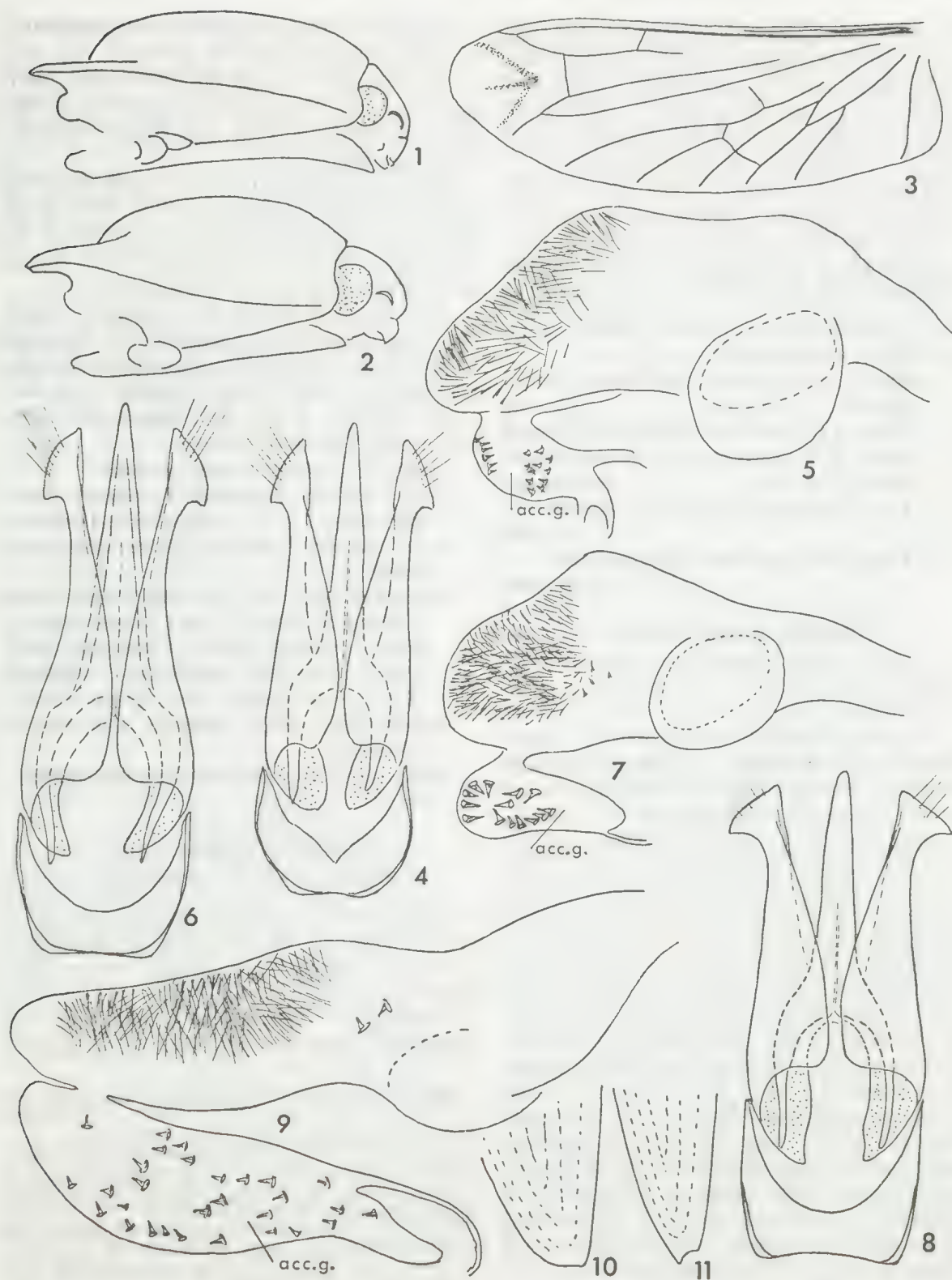
Ophidius vericulatus sp. n.

Figs. 6, 7, 11. Plate 3, fig. 2.

This species resembles *elegans*, but it is easily separated by the apically bi-pointed elytra, and wider black median line on pronotum.

Head black with shallow triangular central depression; antennae serrate but segments

Figs. 1-11. 1.—*Ophidius elegans* Cand. head and prothorax lateral view; 2.—*Yalganus serricornis* (Cand.) head and prothorax lateral view; 3.—*Ophidius histrion* (Boisd.) wing venation; 4.—*Ophidius elegans* Cand. aedeagus; 5.—bursa copulatrix (acc. g.—basal section of accessory gland); 6.—*Ophidius vericulatus* sp. n. aedeagus (holotype ♂); 7.—bursa copulatrix (allotype ♀); 8.—*Ophidius dracunculus* Cand. aedeagus; 9.—bursa copulatrix; 10.—*Ophidius elegans* Cand. apex of elytra; 11.—*Ophidius vericulatus* sp. n. apex of elytra.



somewhat more slender than in *elegans*. Pronotum evenly rounded, densely punctate and covered with dense orange pubescence; the black median line wider and more pronounced than in *elegans*; posterior angles black. Scutellum raised to an almost cordiform platform, with transverse depression near the posterior edge. Elytra orange-brown, bi-pointed apically, the median point being shorter.

Aedeagus slender, apical hooks of lateral lobes with distal margin evenly curved; the female bursa copulatrix with a dense group of long chitinous spines at the base and short triangular spines in accessory gland.

Length 17-24 mm; width 4.5-6.5 mm.

Type material: Holotype ♂ (T-4573) Eubenangee, N.Qld., Jan. 1950, C. Oke (NMV); allotype ♀ (T-4574) Kuranda, N. Qld., Feb. 1953, J. G. Brooks (ex F. E. Wilson Coll. NMV). 2 paratypes (T-4575-T-4576) Kuranda, N. Qld., Feb. 1951 and Jan. 1952, J. G. Brooks (ex F. E. Wilson Coll. and E. T. Smith Coll. NMV); 1 ♀ paratype Mt. Molloy, N. Qld. 7-10 Jan. 1962, H. Demarz (MF); 2 ♂ paratypes Cairns distr., N. Qld. F. P. Dodd (SAM); 1 ♂ paratype (T-4577) Cairns, N. Qld. Mar. 1902 (NMV); 7 ♂ paratypes Kuranda, N. Qld. G. E. Bryant, Nov. 1909 (BM); 2 paratypes Kuranda, Jan. 1950, J. G. Brooks (JGB).

Distribution: North Queensland.

***Ophidius dracunculus* Candèze**

Figs. 8, 9. Plate 3, fig. 3.

Ophidius dracunculus Candèze, 1863: 205; Neboiss, 1956: 55.

This species is easily recognized by its characteristic colour pattern of four pairs of yellowish-brown spots on elytra; it could not be mistaken for any other Australian species.

Head black with distinct triangular depression, in the centre of which is a slightly elevated ridge. Antennae serrate, individual segments slender. The surface of pronotum uneven, coarsely punctate, slight longitudinal depression on either side of the broad elevated middle rise, colour black with yellowish-brown margins.

Scutellum black, vertically elevated with dome-shaped apex, coarsely punctate. Elytra

gradually curved to conjointly rounded apices. Legs short, dark brown to black.

In aedeagus the lateral lobes with apical hooks short, triangular. The female genitalia with basal part of the accessory gland very large, irregularly covered with short and broad spines; bursa copulatrix with a group of long chitinous spines and pair of short ones more distally, the enlarged basal section of accessory gland with stout irregularly situated spines.

Length 13-21 mm; width 3-5 mm.

Type location: BM. The species has been described from specimens in the Chevrolat, Schaum and Guérin-Meneville collections, most of which through various channels were deposited in the Museum d'Histoire Naturelle, Paris, British Museum (Natural History), London and the Institut Royal des Sciences Naturelles de Belgique, Brussels respectively. A specimen from the British Museum, London with the labels "Janson Coll. ex Candèze" and a pink-edged label "*Ophidius dracunculus* Cdze. Austr. septent." in Candèze's handwriting has been examined and is here selected as Lectotype. Three specimens in IRScNB labelled "Types" with locality label "Australie" could only be regarded as paratypes.

Type locality: "Australie septentrionale".

Specimens examined: (72) New South Wales—Gosford, Wollongong, Sydney, Wentworth Falls, Wahroonga (Dec.), Illawarra (Jan.), Blackheath (Jan.), Blue Mountains; Otford (Dec.), Rosebank (Jan.), Mittagong (Jan.), Roseville (Nov.), Hazelbrook (Dec.), Rivertree, Woronora Dam (Dec.). Queensland: Mt. Tambourne (Dec.), National Park, Eukey (Jan.).

(ANIC; BM; CAS; DANSW; HU; NMV; MACL; QM; QU; SAM).

Distribution: New South Wales, Queensland.

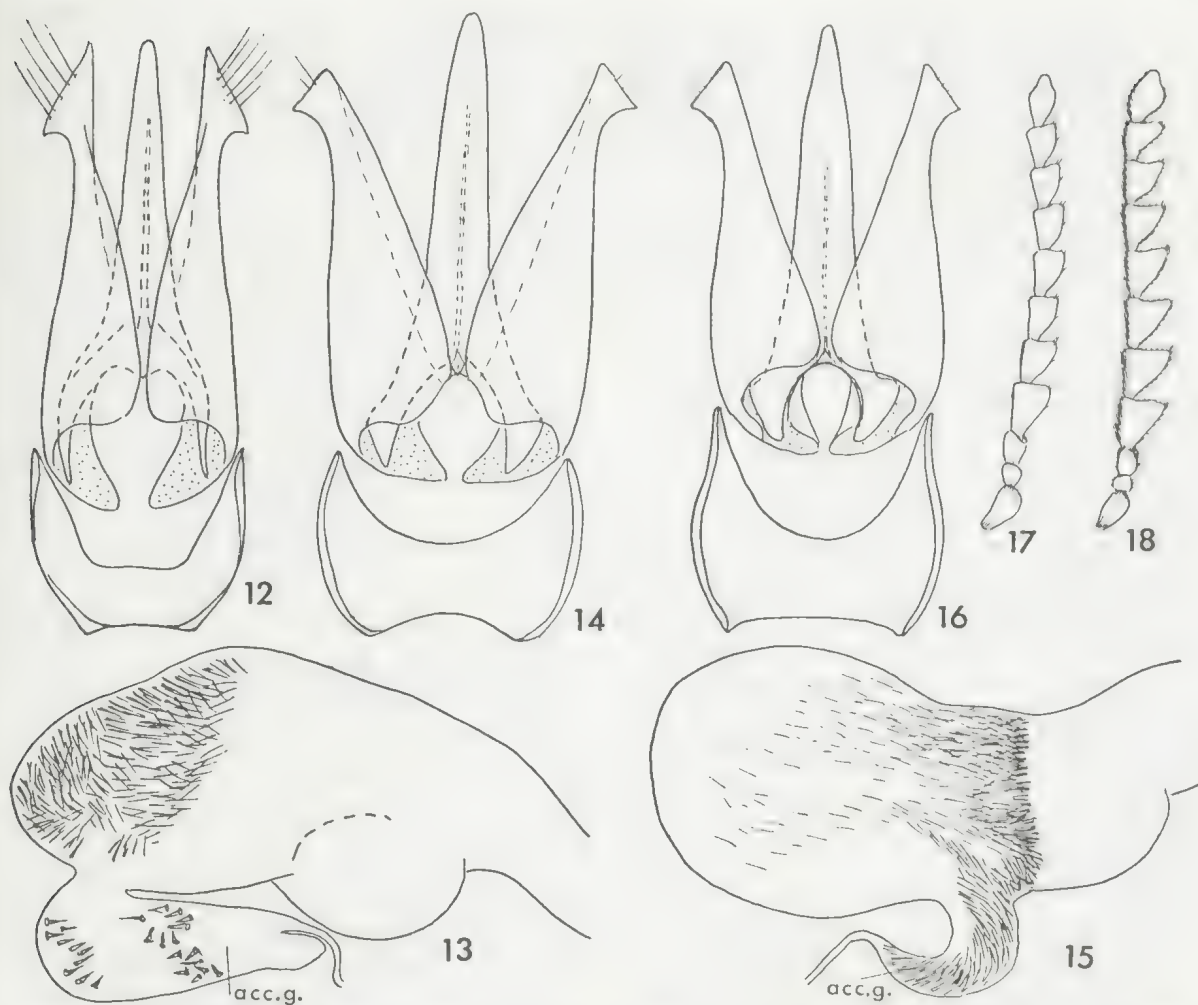
***Ophidius histrio* (Boisduval)**

Figs. 3, 12, 13. Plate 3, fig. 4.

Elater histrio Boisduval, 1835: 105.

Ophidius histrio, Candèze, 1863: 204; Neboiss, 1956: 55.

This species with distinct black and orange-



Figs. 12-18. 12.—*Ophidius histrio* (Boisd.) aedeagus; 13.—bursa copulatrix; 14.—*Yalganus serricornis* (Cand.) aedeagus; 15.—bursa copulatrix; 16.—*Yalganus hirticornis* (Carter) aedeagus; 17.—*Ophidius elegans* Cand. antenna; 18.—*Yalganus serricornis* (Cand.) antenna.

brown curved line pattern does not create any problems with identification.

Head black, with central triangular depression, antennae serrate, almost black with exception of the first few segments which show reddish tinge.

Pronotum broad, evenly rounded, usually with three black longitudinal lines; posterior angles blackish. Scutellum raised vertically, apex in form of an elevated platform with sharply defined margin, the posterior section straight and elevated.

Elytra with distinct blackish curved line pattern on yellowish brown background. In aedeagus the lateral lobes slender with apical hooks somewhat elongate triangular. In female the base of bursa copulatrix densely covered with a group of chitinous spines; the enlarged basal section of accessory gland with two groups of short stout spines.

Length 15-22 mm; width 4-6 mm.

Type location: unknown, described from specimens in Dejean and Dupont collections.

Type locality: "New Holland".

Specimens examined: (93) New South Wales: Sydney, Kurrajong, Illawarra (Jan.), National Park (Dec.), Gosford, Rosebank (Jan.), Gordon (Dec.), Otford,

Acacia Plateau, Comboyne, Ulong (Nov.), Richmond River (Nov.), Dorrigo, Lismore (Dec.), Kew (Jan.), Kangaroo Valley (Jan.), Rivertree, Batemans Bay. Queensland: Mt. Tambourine (Nov.), Springbrook, National Park (Jan.), Stanthorpe (Dec., Jan.), Brisbane, Southport (Jan.), Glen Lamington, Montville (Feb.), Bunya Mtns. (Feb.), Mt. Spec (Jan.).

(ANIC, CAS, DANSW, DEI, HU, JGB, MACL, NMV, QM, SAM).

Distribution: New South Wales, Queensland.

Genus YALGANUS gen. n.

Type species: *Ophidius serricornis* Candèze (present designation).

This genus has been erected to include two species, one of which—*serricornis* is transferred from the genus *Ophidius*, the other—*hirticornis* from the genus *Dicteniophorus*. This genus is rather similar to *Ophidius*, to which it may be closely related, but lacks the tarsal pads, and has the dorsal carina diverging from lateral carina in the pronotum (Fig. 2). The vertically raised scutellum separates it from the genus *Dicteniophorus*.

Generic diagnosis:

Head convex, without or with only slight central depression; frontal carina distinct at sides above the antennae, but incomplete at the centre; mandibles robust, bluntly bicuspid at apex; maxillary palp with terminal segment hatchet shaped. Antennae short, barely reaching posterior angles of pronotum, covered with short, stiff, bristle-like hairs; seg. 1 large, robust, somewhat bulbous; seg. 2 very short, rounded; seg. 3 slightly longer than seg. 2; segs. 4-10 short, triangular, laterally flattened, terminal segment more or less elongate with lateral incision near apex.

Pronotum short, widening posteriorly, with only slight indication of median line, surface covered with short, stiff, bristle-like hairs; posterior angles short, dorsal carina short, diverging from lateral margin.

Scutellum raised similarly to that in *Ophidius*, but the apex not distinctly flattened; surface punctate. Elytra gradually curved, covered with short, bristle-like hairs. Meso-

sternum with highly raised posterior margin and low flattened anterior section.

Legs moderately short, tarsal segments 1-4 becoming shorter distally, not widened, with dense yellowish pubescence beneath, but without pads.

Key to species of the genus *Yalganus*.

1. Pronotum with black ovoid central marking (S. Qld. and NSW) *serricornis*
- Pronotum concolorous orange-brown (N. Qld.) *hirticornis*

The generic name is derived from the word "yalgan" meaning "sun" and used by the Australian aboriginal tribes which lived in Tweed River area of New South Wales.

Yalganus serricornis (Candèze) Comb. nov.

Figs. 2, 14, 15, 18, Plate 3, fig. 5.

Ophidius serricornis Candèze, 1878: 171, Neboiss, 1956: 55.

The species is distinguished by its characteristic colouring. The antennae, head, a central oval marking and the posterior margin of the pronotum, scutellum, legs and the underside of the body all black, sides of pronotum and the elytra orange-brown.

The antennae are short, serrate, segments 4-10 short, triangular, laterally flattened; head with faint central depression; scutellum raised vertically, apex truncate. Pronotum and elytra densely covered with short bristle-like hairs, the latter rounded apically, sutural carina ending bluntly.

In the aedeagus lateral lobes stout, broad at base, terminating with small triangularly shaped apical hook. In female genitalia the bursa copulatrix with an encircling band of long chitinous spines, gradually decreasing in density towards the base; the enlarged basal section of accessory gland densely covered with similar spines.

Length 14-18 mm; width 4-6 mm.

Type location: IRScNB.

Type locality: Sydney.

Specimens examined: (6) New South Wales: Ropes Creek, East Hills.

Queensland: Brisbane, Eungella (Jan.), Rockhampton (Dec.).

(ANIC, IRScNB, JGB, NMV, QU).

Distribution: New South Wales, Queensland.

Yalganus hirticornis (Carter) comb. nov.

Fig. 16. Plate 3, fig. 6.

Dicteniophorus hirticornis Carter, 1939: 323; Neboiss, 1956: 61.

Among species included in the genus *Dicteniophorus* Candèze, *hirticornis* was the only one with a typical vertically raised scutellum. This, as well as the shape of posterior angles of the pronotum, the clothing of bristle-like hairs and the position of dorsal carina indicated its closer relationship to *serricornis*.

Concolorous orange-brown species, the head, antennae, posterior margin of pronotum, scutellum, the underside of the body and legs black. Pronotum and elytra densely covered with short bristle-like hairs. Elytra with sutural carina ending acutely. Scutellum raised vertically, apex as somewhat flattened dome, surface punctate.

The aedeagus very similar to that of *serricornis*, characterized by small triangularly shaped apical hooks on lateral lobes. Female not dissected.

Length 18-21 mm; width 5-6 mm.

Type location: AM.

Type locality: Holotype ♂ Johnstone Riv. Qld. H. W. Brown, labelled "*Dicteniophorus pilosicornis* Cart." an unpublished name which was changed to *hirticornis* in the final manuscript. Paratype ♀ (not ♂ as stated in the description) same locality as holotype.

Specimens examined (5) Queensland: Cairns (Feb.), Kuranda (Nov.).

(AM; BM; NMV).

Distribution: North Queensland.

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Acknowledgements

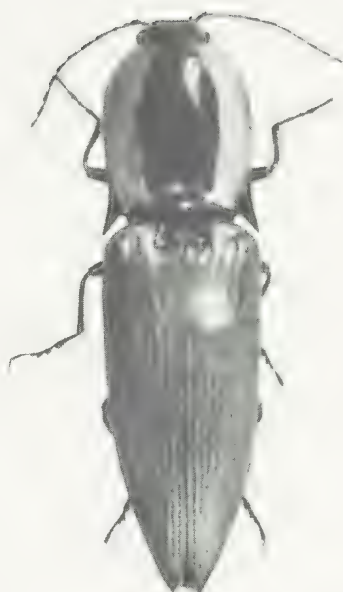
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PLATE 3

1. *Ophidius elegans* Cand. Stanthorpe, Q.
2. *Ophidius vericulatus* sp. n. Paratype T-4575 Kuranda, Q.
3. *Ophidius dracunculus* Cand. Mittagong, N.S.W.
4. *Ophidius histrio* (Boisd.). Gosford, N.S.W.
5. *Yalganus serricornis* (Cand.). Queensland.
6. *Yalganus hirticornis* (Carter). Cairns distr., Q.



1



2



3



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6

THE FOSSIL CRAB

OMMATOCARCINUS CORIOENSIS (CRESSWELL)

and a review of related Australasian species

By R. J. F. JENKINS

Department of Geology and Mineralogy, University of Adelaide

Summary

Ommatocarcinus corioensis (Cresswell), distinctive for its elongate eyestalks and chelipeds, occurs widely in the marine Lower Miocene to Pliocene of southeastern Australia and is particularly abundant in the late Lower and Middle Miocene. It is apparently ancestral to the extant Australian *O. macgillivrayi* White, both being characterized by a pterygostomial stridulating ridge. Regression analyses show that in each the growth of the male chelae is positively allometric with respect to the carapace. The living New Zealand *O. huttoni* Filhol, which lacks a pterygostomial stridulating ridge, evidently represents a separate lineage.

O. corioensis occurs in association with fossil burrow complexes which closely resemble the dwelling burrows of its extant, European, near-relative *Goneplax rhomboides* (Linné). It was a neritic species; its times of greatest abundance relate to oxygen isotope temperatures of 14 to 17° C and the prevalent deposition of relatively fine grained sediments favourable to its burrowing habits.

Fossil species of *Ommatocarcinus* White occur in the Middle Eocene of Spain and the Neogene of Australia and New Zealand. Extant species are found in the Indo-West Pacific region, including Natal. The genus is considered ancestral to *Goneplax* Leach.

Introduction

Cresswell (1886) gave a short description of a fossil crab he named *Gonoplax corioensis*, obtained from nodules collected at Curlewis and North Shore near Geelong, Victoria. Hall (1905) redescribed the species and correctly referred it to the genus *Ommatocarcinus* White. While Hall's description is sufficiently detailed to characterize the species, it fails to describe the ventral parts of the crab, says little about the ambulatory legs, and is inadequate for the identification of the very fragmentary remains frequently encountered.

Since the time of Hall's description numerous new specimens of the fossil crab, some unusually well preserved and remarkably complete, have been obtained from a variety of localities. In the same period, studies by many workers have greatly increased knowledge of the Tertiary stratigraphy of southern Australia. This paper aims to provide a detailed description of *O. corioensis* and to analyze its systematic position relative to the other described species of *Ommatocarcinus*, particularly the living Australian *O. macgillivrayi* White, 1852. The stratigraphic distribution of *O. corioensis* is reviewed in the light of the new finds, and

information concerning its palaeoecology is presented.

The available descriptions of *O. macgillivrayi* omit details of potential diagnostic significance and in an attempt to correct this a new description is provided. New illustrative material and also a diagnosis are given for the extant New Zealand *O. huttoni* Filhol, 1885, which was recently redescribed by Takeda and Miyake (1969).

The depositories of the fossil and recent materials studied are as follows:

National Museum of Victoria, Melbourne, Victoria (N.M.V.).

Geology Department collection, The University of Tasmania, Hobart, Tasmania (T.U.).

Palaeontological collection, Department of Geology and Mineralogy, The University of Adelaide, Adelaide, South Australia (A.U.).

The Australian Museum, Sydney, New South Wales (A.M.).

The Queensland Museum, Brisbane, Queensland (Q.M.).

Dominion Museum, Wellington, New Zealand (D.M.).

Systematics

Order Decapoda

Family Goneplacidae MacLeay, 1838

Subfamily Goneplacinae MacLeay, 1838

Genus OMMATOCARCINUS White, 1852.

Ommatocarcinus White, 1852: 393. H. Milne-Edwards, 1852: 163. Miers, 1886: 246. Stebbing, 1893: 92. Alcock, 1900: 280, 293. Tesch, 1918: 181, 186. Barnard, 1950: 282, 285. Glaessner, 1960: 28; 1969: R525. Bennett, 1964: 74. Guinot, 1969: 523. Takeda and Miyake, 1969: 173-175. Vía, 1970: 310-311, 314-316.

Neommatocarcinus Takeda and Miyake, 1969: 173-175.

Glaessneria Takeda and Miyake, 1969: 175.

(non) *Glaessneria* Wright and Collins, 1972: 34.

Type species: *Ommatocarcinus macgillivrayi* White, 1852, by monotypy.

Diagnosis

Carapace trapezoidal or pentagonal, its width between tips of large, single extraorbital spines more than 1.6 times length; front narrow, less than 1/4 width of carapace between tips of extraorbital spines, usually deflexed and more or less truncate; inner-orbital notches generally well indented; orbits elongated transversely, trough-like to accommodate greatly elongated eyestalks; extraorbital spines usually directed laterally; pterygostomial regions with an anterior ridge which may or may not be transversely ribbed for stridulating. Basal three segments of male abdomen occupying all of width between coxa of last pereopods or reduced in width. Chelipeds, particularly those of males, usually sub-equal and strongly elongated, with palms compressed and fingers elongate. Ambulatory legs slender.

Remarks

Miers (1886) considered *Ommatocarcinus* closely allied to *Goneplax* Leach. Both genera are characterized by having the fronto-orbital margin the widest or nearly the widest part of the carapace, the orbits trough-like for accommodating greatly elongated eyestalks, the anterolateral angles produced to a spine, and the chelipeds elongated. Tesch (1918) and Bennett (1964) indicated that some members of both genera have the basal segments of the male abdomen reduced in width, not occupying the full distance between the coxa of the last pair of legs as suggested by Miers.

Ommatocarcinus differs from *Goneplax* in having a relatively narrower front which generally has well defined inner-orbital notches. The more typical forms of *Ommatocarcinus* have the extraorbital spines strongly produced and directed laterally, not short and forwardly directed as in *Goneplax*. Apparently no members of *Goneplax* have a stridulating device.

Takeda and Miyake (1969) split *Ommatocarcinus* into *Ommatocarcinus* White and two new genera, *Neommatocarcinus* (type species *O. huttoni* Filhol, 1885) and the monotypic *Glaessneria* (type species the fossil form *O. arenicola* Glaessner, 1960). *Neommatocarcinus* is distinguished from *Ommatocarcinus* on the basis of details of its sub-frontal features and antennules, the form of its buccal cavern and third maxilliped, the absence of a pterygostomial stridulating ridge, and most importantly, the form of the male abdomen, which is narrowed with several segments fused. The fossil form *O. zariquieyi* Vía, 1959, from the Eocene of Spain, is also referred to *Neommatocarcinus* because it shows a similar fusion of abdominal segments.

O. macgillivrayi and *O. huttoni* are herein compared in plate IV. A number of the differences on which Takeda and Miyake base *Neommatocarcinus* are quite minor, notably the lengths of the antennules and variation in the maxillipeds. The high crest on the epistome of *O. huttoni* is an exaggeration of the same feature in *O. macgillivrayi*. The development of stridulating devices may be variable amongst species of a single genus such as in *Ovalipes* Rathbun (Stephenson and Rees, 1968; Stephenson, 1969). Crabs show a persistent evolutionary trend towards reduction of the abdomen (Glaessner, 1960) and such simple evolutionary steps as the narrowing and fusion of abdominal segments might potentially occur in a number of quite separate species lineages. Thus while the differences between *O. macgillivrayi* and *O. huttoni* are of undoubted significance at the species level, there seems little real justification for a generic separation which leads only to a proliferation of names in the literature.

O. arenicola, the type of *Glaessneria*, is known only from a single mould lacking detail, and at the present very imperfect state of

knowledge concerning it, referral to a new genus seems quite unwarranted. Takeda and Miyake claim that the "contour" of its carapace is distinctive, but this feature is quite variable in the goneplacid genus *Carcinoplax* H. Milne-Edwards (Imaizumi, 1961). In the outline of its carapace *O. arenicola* resembles *O. fibriophthalmus* Yokoya, 1933, and there seems no obvious reason to preclude it from *Ommatocarcinus*.

***Ommatocarcinus corioensis* (Cresswell, 1886)**

Fig. 1A-E, Fig. 7A,B, Fig. 9, Pl. 4 figs. 1-8, Pl. 5 figs. 1a-10.

Gonoplax corioensis Cresswell, 1886: 90, 91.

Ommatocarcinus corioensis (Cresswell) Hall, 1905: 356-360, pl. 23, figs. 1-5. Chapman, 1914: 247, fig. 120B. Glaessner, 1960: 29, fig. 12c; 1969: R525, fig. 334. Takeda and Miyake, 1969: 175. Via, 1970: 3-14.

Diagnosis

Carapace trapezoidal with two transverse ridges; anterior margin of front gently sinuous, slightly concave on either side of a median convexity; supraorbital margins with inner part acute and outer part subrounded in profile, a row of spinules along the whole length; extraorbital spines laterally directed, strongly produced, and narrow based; well developed anterolateral rises, coarsely granulate. Basal segment of eyestalks concealed. Pterygostomial regions with a stridulating ridge bearing numerous short transverse striae. Male abdomen seven-segmented; first three segments just reaching coxae of last pereopods. Mature cheliped meri with a basal stridulating plectrum, an evenly spaced row of spinules on anterior margin, three spinules on distal part of ventral margin, and a spinule half way along dorsal margin.

Material

Over one hundred and seventy specimens, including the types in the National Museum of Victoria, were examined.

The lectotype, here designated as N.M.V. No. P7665, is in a water-rounded phosphatic nodule collected by the Rev. A. W. Cresswell at Curlewis near Geelong, Victoria. Specimen N.M.V. No. P7666, also in a nodule collected

by Cresswell at Curlewis, is designated a paralectotype.

Three hypotypes of Hall (1905), ♂, N.M.V. No. P7667, ♀ N.M.V. No. P7668, N.M.V. No. P7669, are from (the Port Campbell Limestone) Two Mile Beach, Port Campbell, Victoria.

Occurrence and Stratigraphic Position

This species is known from numerous widely distributed localities in southeastern Australia (including Tasmania) and also from the upper part of the continental slope off northern New South Wales. Its occurrence is outlined in detail in a following section of this work entitled 'Preservation and stratigraphic distribution of *O. corioensis*', pp. 48-52.

Age

Lower Miocene to Pliocene, particularly common in the late Lower Miocene and Middle Miocene.

Description

The trapezoidal carapace is widest from tip to tip of the strongly produced, laterally directed extraorbital spines; the dorsal surface is slightly arched transversely, but sagittally slopes moderately down to the anterior and posterior from a flattish transverse median area.

The front is deflexed and narrow, between one sixth and one seventh the width of the carapace between the tips of the extraorbital spines; its anterior margin is almost straight except for a gentle concavity on either side of a slight median convexity. The front has a border which is very narrow on the anterior margin, but considerably wider adjacent to the inner-orbital notches where it bears a shallow groove containing a row of pits.

The supraorbital margins slant rearwards a little, are slightly convex at the innermost part, but otherwise nearly straight; they bear a single row of spinules. The spinules are short and close-spaced on the acute inner third of each supraorbital margin, but become longer and more widely spaced on the outer two thirds, which is subrounded.

The extraorbital spines are narrow based

with their hind margin rather abruptly curving to the lateral regions of the carapace. The hepatic regions and the upper surface of the extraorbital spines bear distinct granules.

The nearly vertical anterolateral regions are anterior to distinct lateral rises which are directed slightly upwards and densely covered by coarse granules. The postero-lateral regions slope steeply downwards and outwards to meet the pleural sutures of the carapace and are markedly convergent rearwards. The slightly concave posterior margin has a prominent posterior border.

The carapace is divided dorsally into three subequal flattish parts by a distinct ridge extending between the lateral rises, and a shorter ridge arched towards the anterior over the front of the cardiac region. The ends of the anterior ridge curve posteriorly, its central part is pitted and the distal ends bear small granules. Two depressions lie just anterior to the curve of the ridge and a third depression notches it near its termination.

Most of the regions on the dorsal part of the carapace are slightly tumid and are separated by shallow grooves. The mesogastric region is raised, sub-triangular, with an anterior prolongation. The urogastric region is depressed and constricted; it is delimited laterally by deep grooves which are convex inwards. The cardiac region is trapezoidal, widest anteriorly. The intestinal region is gently arched; its antero-lateral extent is marked by broad depressions. Distinct longitudinal crests are formed at the junction of the dorsal mesobranchial regions and the sloping posterolateral regions. These crests converge slightly towards the posterior and bear distinct oval tubercles, elongate in a transverse direction. The outer part of the branchiocardiac furrow is broad and shallowly depressed; the inner part consists of several depressions, the most marked of which is the deep curved groove at the side of the urogastric region.

Most of the dorsal surface of the carapace is minutely granulated; there is a gradation into the regions of coarse granules described above. The posterior border is smooth. Depressions and pits on the exterior of the carapace corre-

spond to muscle attachments on the interior surface (Fig. 1C).

The orbits form long narrow trenches; they open to the subfrontal region via notches containing the antennal bases. The suborbital margins are concave except for the innermost part which projects bluntly forwards and curves downwards just lateral to the notch for the antennae. The inner two thirds of each sub-orbital margin have an acute profile and one line of more or less distinct granules.

The eyestalks (one only shown, Fig. 1A) are slender and elongate with the base of the corneae apparently a little beyond the tips of the extraorbital spines. The base is expanded; the first segment is not exposed.

The antennule bases lie close together near the subfrontal median septum which is shaped like an inverted 'Y'. The epistome is wide with the hind margin mainly concave except for a small central projection and a slight notch half way between the centre and the lateral margin.

A curved stridulating ridge with about 76 transverse ribs is situated on the anterior part of the pterygostomial region. The buccal frame is more broad than long with the sides nearly parallel.

The ischium of the third maxilliped (Fig. 1D) is as broad as it is long, convex inwards, concave exteriorly, and with a prominent basal projection directed laterally. The merus is sub-quadrate, wider than long, with the lateral anterior angle abruptly rounded. The palp is imperfectly known. The exopodite is gently arched inwards and reaches a little more than the middle of the merus; there is a small lateral projection at the base.

The sternum is somewhat rounded, broader than long, with the posterior straight. The anterior segment is large, broad, and sub-pentagonal with the posterior an obtuse angle. The second and third segments are subequal, the fourth is half as long again as each of the second and third segments, and the fifth is reduced. The first four segments have crescentic episterna extending back adjacent to the next posterior sternite and forming the anterior boundary of the socket for the coxa of the limb

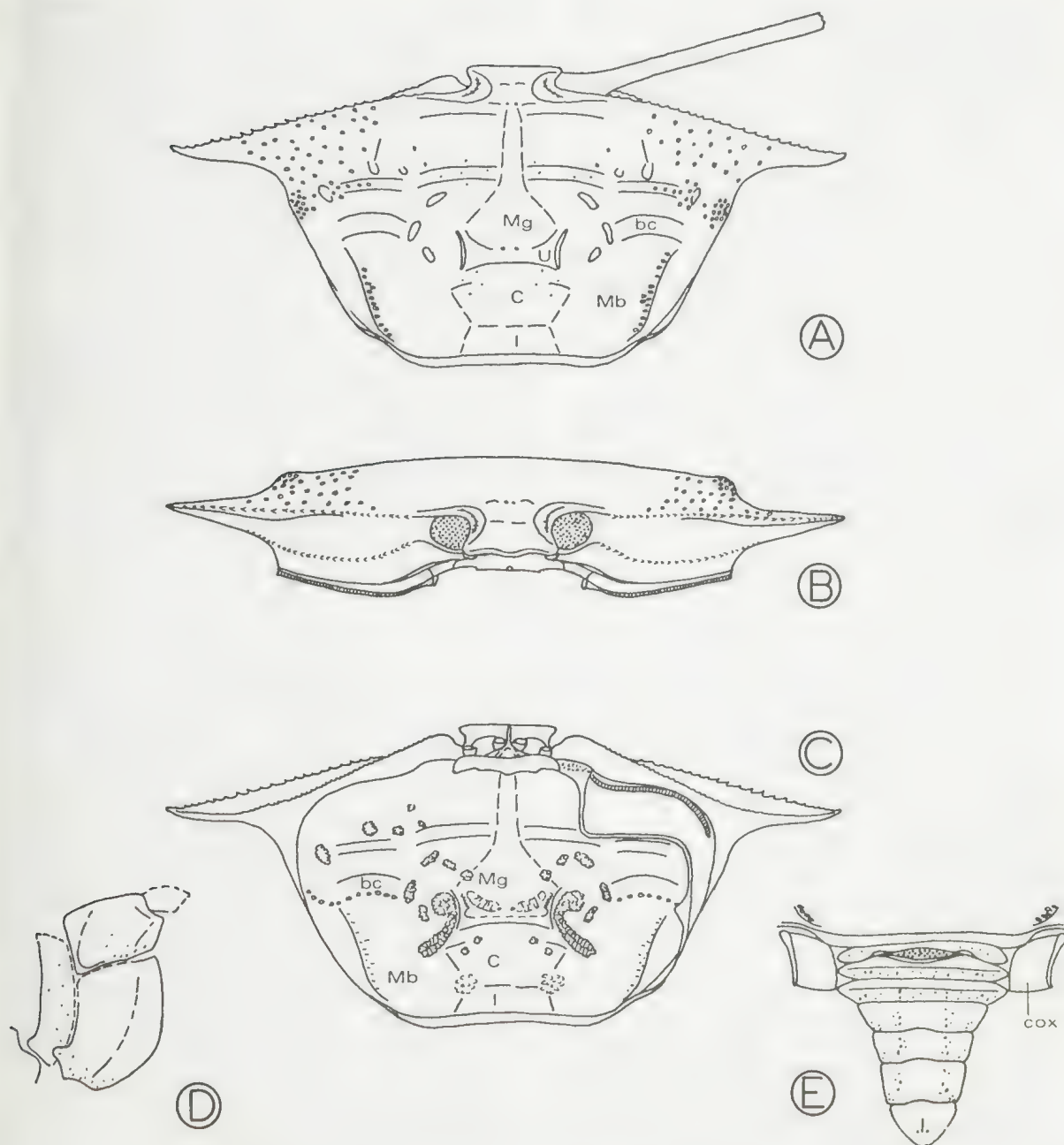


FIGURE 1

***Ommatocarcinus corioensis* (Cresswell)**

A-C, reconstruction of carapace. A, dorsal view with regions of carapace lettered; Mg, mesogastric; U, urogastric; C, cardiac; I, intestinal; Mb, meso-

branchial; bc, branchiocardiac furrow. B, anterior view. C, ventral view with right pterygostomial-brachistegal plate removed. All $\times 1\frac{1}{2}$. D, reconstruction of right third maxilliped, ventral view: $\times 3$. E, reconstruction of male abdomen; cox, coxa of fifth pereopod: $\times 1\frac{1}{2}$.

of the next somite. The surface of the sternum is sparsely pitted.

The abdomen is in seven segments; the three basal segments extend the full distance between the coxae of the last pereopods in mature individuals of both sexes. The first three segments of the male abdomen (Fig. 1E) have the lateral portions tapered and rounded; later segments are progressively narrow towards the rounded, triangular telson. The female abdomen has the lateral portions of the second and third segments rounded, the fourth to sixth segments decreasing only slightly in width, and the telson broad and semi-circular.

The chelipeds are elongate and sub-equal. The short coxae are pitted near the ventral, distal margin. The ischia have an anterior ridge which is produced and expanded distally to a blunt protuberance. The meri are narrow, elongate, slightly arched towards the anterior, and have a rounded-triangular cross-section with the dorsal and ventral margins distinctly granulated. On the proximal dorsal part of the meri, just anterior to a basal V-shaped suture, three small ridges are opposed to the pterygostomial stridulating ridge. Nine to twelve evenly spaced spinules are situated on the anterior margin, one short blunt spine is midway along the dorsal, and three spinules are positioned on the distal part of the ventral margin of each merus. The carpi are globular, with a short anterior border, a stout internal spine and an external spinule. The marginal areas are granulated. The palms are compressed, and widest between the rounded dorsal and ventral margins. A slight sulcus is on the ventral part of the outer face, and the inner face has a broad longitudinal ridge. The dorsal and ventral margins and the ridge on the inner face are distinctly granulated; a line of several spiniform granules is on the distal part of the inner face near the dorsal margin. The fingers are elongate, curved and somewhat laterally compressed with shallow, median, longitudinal grooves. The prehensile margins have sub-triangular or rounded teeth. Rows of pits are situated near the teeth and in the median, longitudinal grooves.

In large males the extended length of one cheliped may be nearly twice the width of the

carapace between the tips of the extraorbital spines. The palms are rather narrow, but broaden distally where the ventral margin is compressed. The right palm is slightly broader than the left; there is a slight gap between the bases of the right fingers, but none between the left. The proximal teeth on the right fingers are rounded; the distal teeth are acute. On the left fingers the teeth are separated and acute with sharp margins. The finger tips of both hands are curved to form pincers.

The chelipeds of the female are shorter than those of the male. The palms are relatively broader and shorter with the ventral margin straight or gently convex and compressed. The right fingers are hardly separated at the base, but the proximal teeth are rounded as in the male. The teeth of the left fingers are not separated. Terminal pincers are not well developed on the fingers of either hand.

The ambulatory legs increase in length in the order 1, 4, 2, 3. The longest is about one and a quarter times the width of the carapace between the tips of the extraorbital spines. The coxae are sub-quadrate with a row of pits on the ventral, distal margin. The meri are compressed and fusiform, widest medially, and about a quarter as wide as long; the outer half of the dorsal margin is finely granulated and bears one to three distal spinules. The carpi are half the length of the meri; they are arched dorsally and widened distally with the distal part of the dorsal margin produced to form a broad spine. The propodi are compressed and about a quarter as long again as the carpi; they taper slightly and the faces have a longitudinal groove containing several pits. The ventral margins of the propodi of the first and second pairs of legs have a line of pits which probably contained hairs in life. The dactyli are long, curved and tapering with two dorsal longitudinal grooves containing elongate pits.

Several specimens show traces of coloration; the palms are speckled with grey and the tips of the fingers of males are dark coloured.

Dimensions

Measurements are given in Table 1 for three nearly complete skeletons and one other showing the third maxillipeds.

Regression Analysis

Regression analyses have been made on measurements from two collections:

- (a) Male specimens from the late Lower Miocene and Middle Miocene sediments, and the late Miocene or Pliocene phosphatic nodule beds of the Otway Basin, Victoria.
- (b) Male specimens of late Lower Miocene age from the upper member of the Morgan Limestone near Morgan in the South Australian portion of the Murray Basin.

For both these collections analyses were made of the relationships between the length of the cheliped palms and the width of the carapace just behind the base of the extra-orbital spines, and between the length of the cheliped palms and their width. For the numerically larger Victorian collection an analysis was also made of the relationship between the

length of the carapace and its width just behind the base of the extraorbital spines. The original data and their analyses are presented in scatter diagrams, Fig. 2A-C, and Table 2.

For the Victorian males the value of the coefficient of correlation, r , is close to unity for the distribution of X_1, Y_1 , but is rather less for the distributions of X_1, Y_2 and X_2, Y_2 (Table 2). The collection is thus rather variable with respect to the dimensions of the chelipeds. The values of ' r ' are still fairly high in every case and so indicate a marked linearity in the distribution of each of the three sets of data analysed. The slope of the regression lines indicates that the growth relationship between the length of the carapace and its width is not quite isometric, and the lengthwise growth of the cheliped palms is positively allometric with respect to their width and the width of the carapace (Fig. 2A).

TABLE 1

Dimensions of *Ommatocarcinus corioensis* in millimetres

The method of measuring for this and the other species described follows that of Rathbun (1918). The measured specimens are: ♂ from the Port Campbell Limestone at Gravel Point, S.E. of Port Campbell, Victoria, N.M.V. P24721; ♂ from the Port Campbell Limestone, above the notch E. of the Amphitheatre near Port Campbell, N.M.V. P24719; ♀ from the Fyansford Clay, in the left bank of the Barwon River at Section 2B, Parish of Murgheboluc, Victoria, N.M.V. P25987.

	♂, N.M.V. P24721	♂, N.M.V. P24719	♀, N.M.V. P25987
Width of carapace between tips of extraorbital spines	58 (impf.)	54	38 (impf.)
Width of carapace just behind bases of extraorbital spines	43	38	29
Length of carapace	27	24	18
Greatest width of front	8.6	7.4	5.4
Length of palm of right cheliped	—	43	16
Length of palm of left cheliped	51	—	18
Width of palm of right cheliped	—	13	—
Length of right fixed finger	—	16	—
Length of left fixed finger	—	16	—

Lengths of ambulatory appendages of ♂, N.M.V. P24721

	Coxa + basis	Ischium	Merus	Carpus	Propodus	Dactylus
First	—	—	25 (impf.)	10	12	12 (impf.)
Second	—	—	28 (impf.)	12	15	11 (impf.)
Third	—	—	29	12	15	12
Fourth	4.7	2.2	25	12	12	12

Total length from merus to dactylus inclusive

First	59
Second	66
Third	68
Fourth	61

For the Morgan male crabs the slope of the regression lines (Fig. 2C and D) indicates that the lengthwise growth of the cheliped palms is again positively allometric relative to the width of the carapace. The allometry is, however, markedly less than for the Victorian specimens.

Examination of the limited data for Victorian females on Fig. 2B and C suggests that the increase in length of the palms is nearly isometric with respect to their width and to the growth of the carapace. The data for one Morgan female is similar to that for the Victorian females.

Remarks

Cresswell (1886) incorrectly described the eyestalks as being comparatively short and the second pair of ambulatory legs as the longest. Hall (1905) corrected the first error but gave little detail concerning the legs. Hall's work also contains several errors; he describes the 'anterior edge' of the carapace as finely and regularly granulated and the cardiac area as triangular. In the lectotype the spinules on the supraorbital margins are largely covered by sediment or broken and the cardiac region is damaged by a V-shaped fracture. Hall also incorrectly states in his remarks that there is no spinule in the middle of the dorsal margin of the cheliped meri.

Usually, large males have the right chela the major. In approximately one in five specimens

the heterochely is reversed. One specimen, A.U. F17220, in a phosphate nodule from 'Coghills' near Geelong, Victoria, has the left cheliped about half the size of the right. This may be an example of regeneration.

The male crabs from Morgan differ from most of the Victorian males in having somewhat shorter and broader chelipeds. However, several males from Victoria also have short, broad chelipeds. A gradational series appears to exist between the Victoria crabs with long chelipeds and the Morgan specimens. It is thus considered impracticable to separate the two forms. The differences in the chelipeds are shown in the regression analyses.

Ommatocarcinus macgillivrayi White, 1852

Fig. 9; Pl. 5 Fig. 11, Pl. 6 Figs. 1-3,
Pl. 7 Figs. 1, 2a-e.

Ommatocarcinus macgillivrayi White, 1852: 393-394, pl. 5, figs. 1, 1a. H. Milne-Edwards, 1852: 163. Haswell, 1882: 90-91. Balss, 1922: 138. Sakai, 1934: 314, fig. 22; 1936: 137, fig. 96; 1939: 564, pl. 102, fig. 5; 1965: 170, pl. 84, fig. 3. Guinot-Dumortier and Dumortier, 1960: 121, figs. 3, 3a. Glaessner, 1960: 29, fig. 12d. Guinot-Dumortier, 1961: 83, fig. 5. Griffin and Campbell, 1969: 151-153, figs. 4, 6D. Guinot, 1969: 523, figs. 69-70. Takeda and Miyake, 1969: 174. Vía, 1970: 314.
Ommatocarcinus sp. Yokoya, 1933: 198-199, fig. 65A, B.
Ommatocarcinus pulcher Barnard, 1950: 286, fig. 53b-f.
(non) *Ommatocarcinus macgillivrayi* Miers, 1886: 247-248 (= *Ommatocarcinus huttoni* Filhol, 1885).

TABLE 2

Analyses of data indicated on the scatter diagrams comprising Figure 2.
The variables are as explained in the legend of Figure 2.

Number of Items of Data	Variables	Coefficient of Correlation	Equations of Regression Lines	Standard Errors for Regression Coefficients		Standard Errors of Estimate	
20	X_1, Y_1	.98	$Y_1 = .91X_1 - .069$ $X_1 = 1.05Y_1 + .14$	Syx .029	Sxy .033	Sy .0016	Sx .0017
23	X_1, Y_2	.88	$Y_2 = 1.73X_1 - 1.14$ $X_1 = .45Y_2 + .85$.20	.052	.091	.045
19	X_2, Y_2	.91	$Y_2 = 1.45X_2 - .003$ $X_2 = .57Y_2 + .19$.16	.064	.083	.052
7	X'_1, Y'	.94	$Y' = 1.43X'_1 - .78$ $X'_1 = .62Y' + .66$.24	.10	.055	.036
14	X'_2, Y'	.96	$Y' = 1.16X'_2 + .15$ $X'_2 = .79Y' - .028$.10	.069	.050	.041

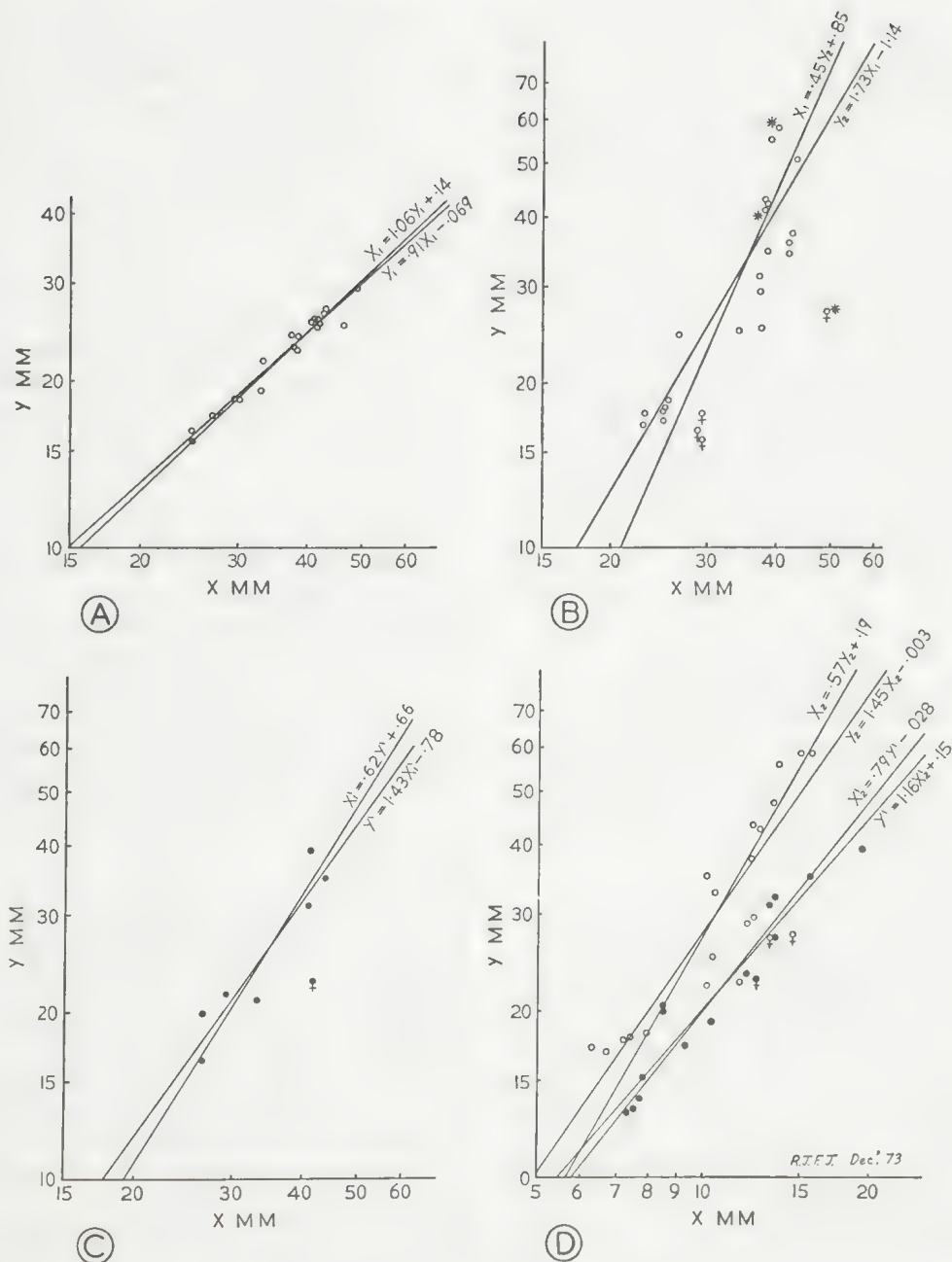


FIGURE 2

Regression analyses for selected dimensions of male specimens of *O. corioensis*.

A: Victorian collection; log width of carapace just behind extraorbital spines, X_1 , on log carapace length, Y_1 , data \circ .

B: Victorian collection; X_1 on log length of cheliped palm, Y_2 , data \circ . Coincident data indicated by an asterisk. Female data shown ϕ , but not included in regression analyses.

C: Morgan collection; log width of carapace just behind extraorbital spines, X' , on log length of cheliped palm Y' , data \bullet . Female data, ϕ , not included in analyses.

D: Victorian collection; log width of cheliped palm, X_2 , on Y_2 , data \circ . Female data, ϕ , not included in analyses.

Morgan collection; log width of cheliped palm, X'_2 , on Y'_2 , data \bullet . Female data, ϕ , not included in analyses.

Diagnosis

Carapace trapezoidal with two transverse ridges; the anterior margin of the front rather straight except for two notches near centre; supraorbital margins of adults rounded in profile and with several rows of granules; extraorbital spines laterally directed, strongly produced, of moderate breadth at base; anterolateral rises weakly developed, finely granulated. Basal segment of eyestalks exposed. Pterygostomial regions with a stridulating ridge bearing some 77 to 85 transverse striae. Male abdomen seven segmented; first two segments reduced in width; third nearly reaching coxae of last pereopods and covering most of external spermiduct. Mature cheliped meri with a basal stridulating plectrum and one spinule half way along dorsal margin; palms compressed for most of length; fingers more than half length of palms and with smooth surfaces.

Type material

Holotype, ♂, from Port Curtis, Queensland; No. 50.11, dried collection, British Museum (Natural History). A second specimen from 'Australia' was registered at the British Museum in 1856 (Dr A. L. Rice, pers. comm.).

Material examined

(a) Extant—

Mature ♂, Q.M. No. W419, Clontarf, Moreton Bay, Queensland.

Mature ♂, A.M. No. P1147, near Sydney, New South Wales.

Three juvenile males, A.M. No. P15171 a and b, A.M. No. P15172, trawled at 80 m depth off Cronulla, New South Wales.

Small ♀, A.M. No. P10090, Sow and Pigs Shoal, Port Jackson, New South Wales.

(b) Fossil and sub-Recent—

Tentatively referred to *O. macgillivrayi*: fragmentary remains of a cheliped N.M.V. No. P24686, upper shell bed in Jemmys Point Formation in road cutting for Princes Highway on W. side of Bunga Creek, 5.5 km E.N.E. of Lakes Entrance, Gippsland, Victoria. The Jemmys Point Formation is Kalimnan (Pliocene).

Palm of major (right) cheliped of prob-

ably a male, Q.M. No. F6620, and two specimens of nearly complete carapace, sternum and fragmentary appendages preserved in concretions, Q.M. No. F6624 and Q.M. No. F6625, dredgings at Lugage Point, N. side of mouth of Brisbane River, Moreton Bay, Queensland.

Distribution

Pliocene—? Gippsland Basin, Victoria.

Sub-Recent—Moreton Bay, Queensland.

Extant—The east coast of Australia, from Port Curtis, Queensland, south to off Cronulla, near Sydney, New South Wales. The species is recorded in 'shoal water' at Port Curtis (White, 1852), occurs in the shallow waters of Moreton Bay (Griffin and Campbell, 1969) and has been taken at 80 m depth off Cronulla.

Japan; from Bōsō Province, Sagami Bay, the Kii Strait, Nagasaki, and near the Koshiki Islands. The species is known from a maximum depth of 150 fath. (274 m) at Yodomi on Sagami Bay (Balss, 1922) and from a minimum of 15-13 m at Mitohama, also on Sagami Bay (Sakai, 1965).

Natal; one specimen from the stomach of a fish (*O. pulcher* Barnard, 1950).

Description

The carapace is similar in outline and general form to that of *O. corioensis*. The front is narrow, one eighth of the width of the carapace between the tips of the extraorbital spines; its anterior margin is truncated with two notches separated by a small, acute rostral projection. The front has a border which is prominent on the anterior margin, and markedly dilated adjacent to the deep inner-orbital notches where it bears a shallow groove containing a line of pits.

The supraorbital margins slant rearwards a little and are gently recurved; they have a bluntly rounded profile and bear two rows of coarse granules and several rows of finer granules on the lateral portion. The supraorbital margins of juveniles have an acute profile and one row of coarse granules. Females and juvenile males have a fringe of hairs ventral to the inner two thirds of each supraorbital margin.

The suborbital margins have a rather acute profile, one row of indistinct tubercles, and a sparse fringe of long hairs. They are concave for most of their length, but the inner part is bluntly produced.

The extraorbital spines are laterally directed, strongly produced, and acute, with the base of moderate breadth and the hind margin smoothly curving to the anterolateral regions of the carapace.

Across the anterior third of the carapace is a prominent transverse ridge, the ends of which curve a little towards the posterior and terminate at weakly developed anterolateral rises. Except for the longitudinal mesobranchial crests being lower and more rounded, the carapace of *O. macgillivrayi* is sculptured very similarly to that of *O. corioensis*. The greater part of the surface of the carapace is smooth or minutely granulated; the upper surface of the extraorbital spines, the hepatic regions, the slight anterolateral rises, and the longitudinal mesobranchial crests bear fine, distinct granules.

The slender and elongate eyestalks reach just beyond the tips of the extraorbital spines; both the proximal portion and the cornea are slightly expanded. The first segment is visible in the inner-orbital notch.

The antennules are situated near the centre of the subfrontal region and fold transversely. They are fairly short and have two cylindrical joints before dividing into two short, hair fringed rami. The antennae have three short joints reaching to the corner of the front and then a many-segmented flagellum as long as the whole of one antennule.

The epistome is transversely elongated with the hind margin gently concave on each side of the centre.

Across the anterior part of each pterygostomial region is a curved stridulating ridge bearing some 77 to 85 short transverse striae. The buccal frame is wider than long and slightly wider in front. The surfaces of the pterygostomial and brachioestegal regions are smooth.

The ischium of the third maxilliped is nearly as wide as it is long and has a distinct lateral projection at the base. The merus is subquadrate, three quarters as long as it is wide,

with an obtuse, rounded anterolateral angle. The inner margin of the ischium and the margins of the merus and palp are fringed with hairs. The curved exognath reaches to the first half of the length of the merus, and has a strong, inwardly directed spine near its distal end and a lateral projection at the base.

The sternum is very like that in *O. corioensis* except for a complete, shallow, transverse groove extending between the anterolateral corners of the first large sternite, and somewhat shorter episterna, which reach less closely to the socket for the pereopod of the next somite.

The abdomen is distinctly seven-jointed; only the ends of the first segment may be exposed from under the carapace. The first and second segments are reduced in width to three quarters the distance between the coxae of the last pereopods so that parts of the underlying sternite are exposed.

In the male abdomen the third segment covers all but the extreme proximal part of the external spermiduct, which lies in a groove between the sternites corresponding to the fourth and fifth pereopods. The fourth to sixth segments taper in width; the longest is the sixth. The telson is triangular with a rounded tip.

The female abdomen tapers only slowly from the third segment and thus is much broader than in the male. The telson is of a broad, rounded, triangular shape.

The chelipeds are subequal and elongate. The cheliped ischia have a finely granulated anterior ridge produced to a blunt, distal spine. The meri are elongate and narrow, are slightly arched anteriorly, and have a rounded triangular cross section. They have fine granules on the ventral margin and coarser granules on the anterior and dorsal margins; a blunt spinule is placed mid-way along the length of the dorsal margin. Anterior to a dorsal 'V'-shaped suture, the proximal part of each merus is slightly expanded and bears a short ridge or keel-like plectrum, which opposes the pterygostomial stridulating ridge. The plectrum has a distinct tubercle near its outer end and a sparse fringe of hairs on the ventral aspect. The carpi are smooth and globular with a few pits in the surface and a single bluntly rounded internal spine. The palms are compressed for most of

their length and are broadest dorsoventrally with a broad ridge on the inner and outer faces and the upper and lower margins rounded. The upper margin and the ridge on the inner face are distinctly granulated; the lower margin is finely granulated. The fingers are elongate, more than half the length of the palms in mature individuals; they are somewhat compressed laterally and have the surfaces smooth except for a serrated line of teeth on the prehensile margin and a row of distinct tubercles posterior to the tooth row on the distal part of the fixed finger.

Juvenile males have several small spines on the distal part of the anterior margin of each cheliped merus; the carpi have an exterior spine. These spines are not present in slightly larger individuals.

In mature males the extended length of one cheliped is between two and two and a half times the width of the carapace between the tips of the extraorbital spines. The palms have the distal part of the ventral margin compressed; the right palm is a little broader than the left. The right fingers have a large diastema at their symphysis, bluntly rounded proximal teeth, and more acute distal teeth. The fingers of the left hand have only a small gap at the base and the teeth are acute and slightly separated. Curved pincers on the tips of both left and right hand fingers cross when the fingers close.

The cheliped carpi of the female have an external spine. The palms are relatively shorter and slightly broader than in a male of comparable maturity, and have the lower margin compressed. There is no large diastema between the fingers of the right hand. The teeth of the left and right hand fingers are not separated and terminal pincers are not well developed.

The ambulatory legs increase in length in the order 1, 4, 2, 3, with the longest about one and a third times the width of the carapace. The form of the legs differs only slightly from that in *O. corioensis*. The meri of the second, third and fourth pairs of legs are finely granulated on the distal half of the dorsal margin. On the distal part are several larger granules and a short spine, not well developed

in males, but prominent in females. The dactyli are compressed dorsoventrally and are curved and narrow with two dorsal grooves containing pits which may or may not hold hairs.

Males have the distal joints of the first and second pairs of legs fringed by hair. The propodi and dactyli of the first pair of legs have two ventral rows of hairs set in pits. A few hairs are present on the third and fourth pairs.

In females the meri and more distal joints of all the legs have fringing hairs.

Heterochely

Normally mature males have the right chela the major.

Dimensions

Measurements are given in Table 3 for the mature male specimen A.M. No. W419 and the female A.M. No. P10090.

Regression analyses

Regression analyses similar to those for *O. corioensis* were made on the five male specimens. The data and analyses are presented in scatter diagrams, Fig. 3A and B, and Table 4. For all the regression analyses 'r' is close to unity, indicating a high positive correlation. The five crabs measured appear to be members of one population.

The slope of the regression lines (Fig. 3A and B) indicates that the growth relationship between the length of the carapace and its width is not quite isometric, and the increase in length of the cheliped palms is positively allometric relative to their width and to the width of the carapace.

Remarks

O. macgillivrayi is the probable descendant of the fossil species *O. corioensis*, from which it differs conspicuously in having the anterior margin of the front doubly notched, not gently sinuous, and the supraorbital margins of the carapace slightly more recurved, rounded in profile rather than acute, and ornamented by several lines of granules, not a single line of spinules. The three basal segments of the abdomen are reduced in width, rather than reaching the full distance between the coxae

of the last pair of legs, and the meri of the chelipeds lack an anterior row of spinules. In *O. macgillivrayi* the basal segment of the eyestalks is exposed; the same segment is apparently covered by the front in *O. corioensis*.

The fragmentary remains of the cheliped from the Pliocene of the Gippsland Basin (N.M.V. No. P24686, Pl. 5, fig. 11) consist of the major part of a left palm and an attached fragment of carpus. While definitely referable to *Ommatocarcinus*, these remains are too fragmentary to be assigned with confidence to any particular species. Nevertheless they markedly resemble the corresponding parts of the chelipeds of males of *O. macgillivrayi*,

particularly in having a distinct longitudinal groove near the upper margin of the palm, and are thus interpreted as providing a tentative Pliocene record of this species. The sub-Recent remains dredged from Moreton Bay do not differ appreciably from the extant form.

O. macgillivrayi has been recorded from Japan by Balss (1922) and Sakai (1934, 1936, 1939, 1965). Specimens of apparently the same Japanese form were described by Yokoya (1933) as *Ommatocarcinus* sp. From a study of literature Griffin and Campbell (1969) conclude that the Japanese crab does not differ significantly from Australian individuals and I concur with this. The dimensions of the carapace and claws of the rather small specimens illustrated by Yokoya and Sakai plot near the regression lines given here (Fig. 3) for the Australian form.

Takeda and Miyake (1969) point out that *O. pulcher* Barnard 1950, from off Natal, South Africa, cannot be distinguished from *O. macgillivrayi* on the basis of the original description and figures and that they may be synonymous.

FIGURE 3

Regression analyses for selected dimensions of male specimens of *O. macgillivrayi* from eastern Australia. A: Log width of carapace just behind extraorbital spines, X_1 , on log carapace length, Y_1 , data \bullet . Female data shown \circ , but not used in analyses.

X_1 on log length of cheliped palm, Y_2 , data \circ . Female data, \circ , not used in analyses. Coincident data marked with an asterisk.

B: Log width of cheliped palm, X_2 , on Y_2 , data \circ . Female data, \circ , not used in analyses.

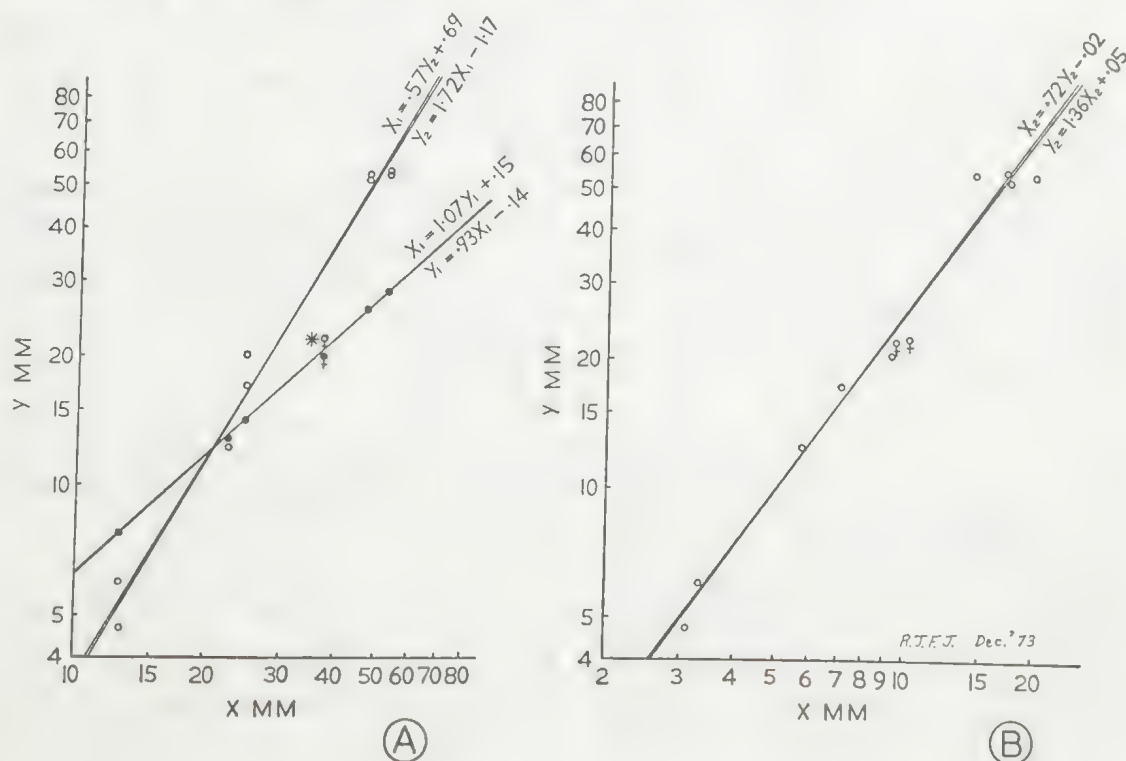


TABLE 3

Dimensions of *Ommatocarcinus macgillivrayi* in millimetres

	♂, Q.M. W419	♀, A.M. P10090
Width of carapace between tips of extraorbital spines	66	49
Width of carapace just behind bases of extraorbital spines	52	37
Length of carapace	27	20
Greatest width of front	8.2	6.1
Length of right cheliped	166	68
Length of left cheliped	162	67
Length of right palm	56	23
Length of left palm	56	22
Width of right palm	20	10
Width of left palm	17	9.2
Length of right fixed finger	32	14
Length of left fixed finger	30	13
Lengths of ambulatory legs: first	73	48
second	82	52
third	84	57
fourth	74	49

TABLE 4

Analyses of data indicated on the scatter diagrams comprising Figure 3.

The variables are as explained in the legend of Figure 3.

Bar above numerals in values for coefficient of correlation indicates figure is not significant.

Number of Items of Data	Variables	Coefficient of Correlation	Equations of Regression Lines		Standard Errors for Regression Coefficients		Standard Errors of Estimate	
			r		Syx	Sxy	Sy	Sx
5	X_1, Y_1	.999	$Y_1 = .93X_1 - .14$.0058	.0067	.0041	.0044
			$X_1 = 1.07Y_1 + .15$					
9	X_1, Y_2	.999	$Y_2 = 1.72X_1 - 1.17$.082	.027	.057	.033
			$X_1 = .57Y_2 + .69$					
9	X_2, Y_2	.998	$Y_2 = 1.36X_2 + .05$.068	.036	.060	.044
			$X_2 = .72Y_2 - .02$					

***Ommatocarcinus huttoni* Filhol, 1885**

Fig. 9, Pl. 7, figs. 3a-c, 4a-b.

Ommatocarcinus huttoni Filhol, 1885: 384-385, pl. 43, figs. 1, 2, 5.*Ommatocarcinus macgillivrayi* White. Miers, 1886: 247-248.*Neommatocarcinus huttoni* (Filhol). Takeda and Miyake, 1969: 175-179 (detailed synonymy), figs. 5 and 6, pl. 2, fig. A.**Diagnosis**

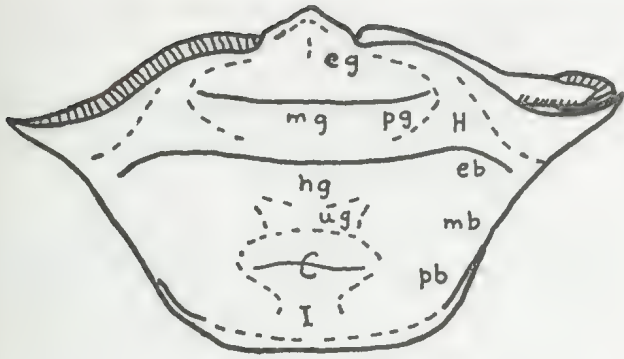
Carapace trapezoidal, fairly broad, without transverse ridges, anterior margin of front gently concave except for a small, acute, rostral projection, supraorbital margins subangular in profile with a line of distinct granules, extra-orbital spines laterally directed, acute, and stout, anterior ridge of pterygostomial regions not adapted for stridulating. Male abdomen reduced in width; third segment not covering external spermiduct; segments 3 to 5 fused.

Adult cheliped meri lacking distinct spinules and without a stridulating plectrum. Mature male cheliped palms with proximal portion narrow and rounded; fingers about one-third length of palms and with surfaces distinctly granulated.

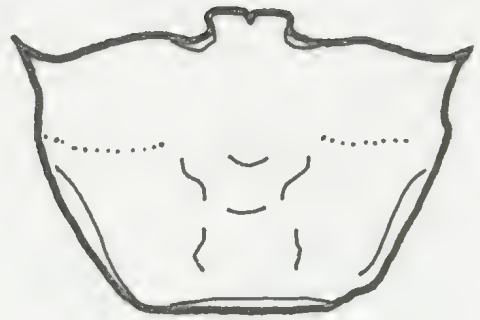
Type material

According to Filhol (1885), his single specimen (holotype) from near Otago, New Zealand, was lodged in the Muséum National d'Histoire Naturelle, Paris.

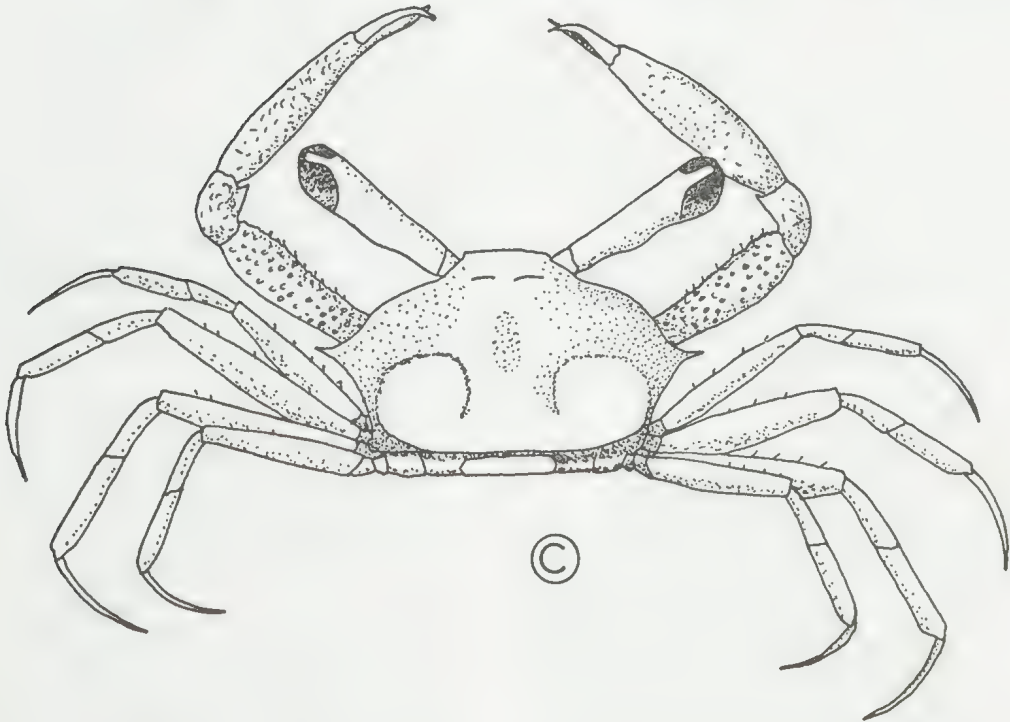
FIGURE 4Other described species of *Ommatocarcinus*:A: *Ommatocarcinus zariquieyi* Vía; carapace, x 3. (After Vía, 1959).B: *O. arenicola* Glaessner; carapace, x 1½. (After Glaessner, 1960).C: *O. orientalis* Tesch; dorsal view, x 10. (After Tesch, 1918).D: *O. fibriophthalmus* Yokoya; dorsal view, x 3. (After Yokoya, 1933).



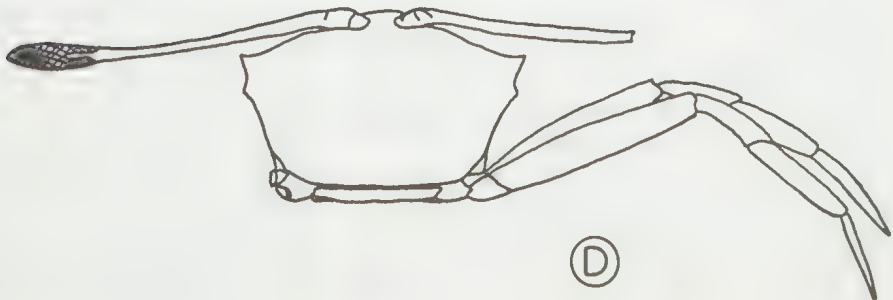
(A)



(B)



(C)



(D)

Material examined

Mature ♂, from 20-28 fath (37-51 m) between 8 and 10 km off Greymouth Bar, west coast of the South Island of New Zealand: D.M. Cr 1765.

Mature ♀, trawled from Cook Strait, New Zealand: D.M. Cr 1171.

Distribution

New Zealand and the Chatham Islands. For details see Takeda and Miyake, 1969.

Remarks

Takeda and Miyake (1969) have described this species in detail and compared and contrasted it with *O. macgillivrayi*.

Other members of the genus

In addition to the *Ommatocarcinus* species described or diagnosed above, the following other forms are known:

O. zariqueiyi Vía, 1959

Figs. 4a and 9

Eocene, Middle Lutetian; Cataluna, Spain.

O. arenicola Glaessner, 1960

Figs. 4b and 9

Otaian to Waiauian, early Lower to Middle Miocene; Waipara River, South Island of New Zealand.

O. sp. Glaessner, 1960

Awamoan, late Lower Miocene; Oamaru, South Island of New Zealand.

O. orientalis Tesch, 1918

Figs. 4c and 9

Near the Kei Islands, at 90 m depth.

O. fibriophthalmus Yokoya, 1933

Figs. 4d and 9

Between Tsushima Island and Gotō Island, Japan, at 146 m.

Recent reviews of these species are given by Takeda and Miyake (1969) and Vía (1970).

Preservation and stratigraphic distribution of *O. corioensis*

Preservation

The materials of *O. corioensis* studied are preserved in one of three ways:

(a) natural skeletal material *in situ* in sediments;

(b) skeletal material enclosed within phosphatic concretions which formed *in situ* in sediments;

(c) skeletal material enclosed within water-worn phosphatic nodules concentrated at the base of certain beds.

The remains preserved *in situ* in sediments almost always have the appendages attached in place and are positioned in a life-like attitude. The inferred significance of this remarkably complete preservation is discussed in a following section on palaeoecology (pp. 52-54). Traces of coloration are sometimes evident in this material.

Examples of the crab within concretions are known from the Miocene at Port Campbell and the Geelong area, and the Pliocene near Hamilton, Victoria. The concretions have a dense, brown or dark coloured centre in which the crabs, other shelly fossils and sand grains are cemented; there is a gradation in the degree of cementation to the enclosing unaltered sediments. The crab remains appear to have served as a nucleus for the diagenetic concentration of phosphatic material which replaced the carbonate minerals in the sediment about the fossil.

Remains of the crab within water-rounded phosphatic nodules are well known from the Geelong area, where localized concentrations of phosphatic nodules occur frequently at the base of the Moorabool Viaduct Sands (Coulson, 1932; Kebble, 1932; Bowler, 1963). About 20 per cent of the nodules in these concentrations enclose fossils of *O. corioensis* or remains of the thalassinid *Ctenocheles* Kishinouye. The preservation of the crabs in the water-rounded nodules is identical to that in the concretions mentioned above. Bowler (1963) considered that the nodules, both with and without crabs, are remanié and represent water-abraded concretions eroded from Miocene and possibly older sediments. This view is accepted here in contradistinction to the suggestion of Coulson (1932) and Kebble (1932) that the crab-containing nodules formed in a mud bed deposited in a transgression postdating the major Miocene phase of deposition, and pre-Kalimnan. Similar

remanié occurrences of the crab in phosphatic nodules occur widely in the Pliocene of southern Victoria and nodules containing *O. corioensis*, and apparently formed in the same way, have recently been dredged from the upper part of the continental slope off New South Wales (von der Borch, 1970; here p. 52). In this paper the terms 'concretion' and 'nodule' are uniformly applied in the sense outlined above.

Stratigraphic distribution

O. corioensis occurs widely in the marine Tertiary sediments of south eastern Australia (Fig. 5). The stratigraphic distribution is outlined in Figure 6 in which the separate occurrences are indicated within the framework of the recognized tectonic-sedimentary basins. The occurrences are as follows:

Murray Basin

Two isolated fingers are from the lower member of Morgan Limestone, section C, Hundred of Cadell, 6 km south of Morgan, South Australia. Early part of *Praeorbulina glomerosa curva* zone of Ludbrook and Lindsay (1969), late Lower Miocene.

Some 25 or so remains are from the top part of the upper member of Morgan Limestone, section C, Hundred of Cadell, near Morgan. Later part of *Praeorbulina glomerosa curva* zone of Ludbrook and Lindsay (1969), latest Lower Miocene.

Four specimens are from Morgan Limestone, near Waikerie, South Australia. Late Lower to earliest Middle Miocene.

Otway Basin

Over 100 remains are from Port Campbell Limestone, sea cliffs in the vicinity of Port Campbell, Victoria; specimens occur in argillaceous limestone above Rutledge's Creek Member and purer limestone near the cliff tops. Localities include: top of London Bridge, cliff top at Point Hesse, Two Mile Beach (Hall, 1905), Gravel Point, notch on E. side of Amphitheatre, mouth of Sherbrook River, cliffs at Beacon Steps (Baker, 1945) and cliffs opposite Sentinel Rock (Baker, op. cit.). *Globorotalia linguaensis*—*Globorotalia mayeri* Zonule to *Globorotalia miotumida* Zonule of

Taylor (in Singleton, 1968; in McGowran et al., 1971); mid Middle Miocene to ?Upper Miocene.

One specimen is from Port Campbell Limestone, Curdies River Lime Works, Curdie, Victoria. ?Middle to ?Upper Miocene.

One specimen is from Port Campbell Limestone, 3 km W. of Timboon, Victoria. ?Middle to ?Upper Miocene.

A number of fragmentary remains are in remanié phosphatic nodules at base of the Grange Burn Formation, Grange Burn, 8 km W. of Hamilton, Victoria. The Grange Burn Formation is Kalimnan or Pliocene (Spencer-Jones, 1971; Taylor, 1971, p. 236). The nodules are probably derived from underlying Miocene sediments.

Two specimens are in phosphatic concretions, Grange Burn Formation, 1 m above (normal?) creek level, Forsyths Bank, Grange Burn. Kalimnan, Pliocene.

One specimen comes from the thin limestone bed 10 m below the top of Fyansford Clay, Amphitheatre on Leigh River, 6 km N. of Shelford, Victoria. *Globigerinoides sicanus* zone of Ludbrook and Lindsay (1969) (data Dr Mary Wade, pers. comm.), late Lower Miocene.

Several remains are in remanié phosphatic nodules, from the base of Moorabool Viaduct Sands, Amphitheatre on Leigh River near Shelford. The Moorabool Viaduct Sands are Upper Miocene (Aziz-ur-Rahman and McDougall, 1972). The nodules are probably derived from the underlying Fyansford Clay.

Two specimens are in phosphatic concretions, from a thin sandy limestone interbed in Fyansford Clay, 0.5 km N.E. of the junction of Bruces Creek and Barwon River, near Murgheboluc, Victoria. Start of *Orbulina universa* zone of Ludbrook and Lindsay (1969) (data Dr Mary Wade, pers. comm.); early Middle Miocene.

Two specimens come from the Fyansford Clay, left bank of Barwon River, section 2B, Parish of Murgheboluc, Victoria. Start of *Orbulina universa* zone of Ludbrook and Lindsay (1969), early Middle Miocene.

Specimens are reported to occur in a thin

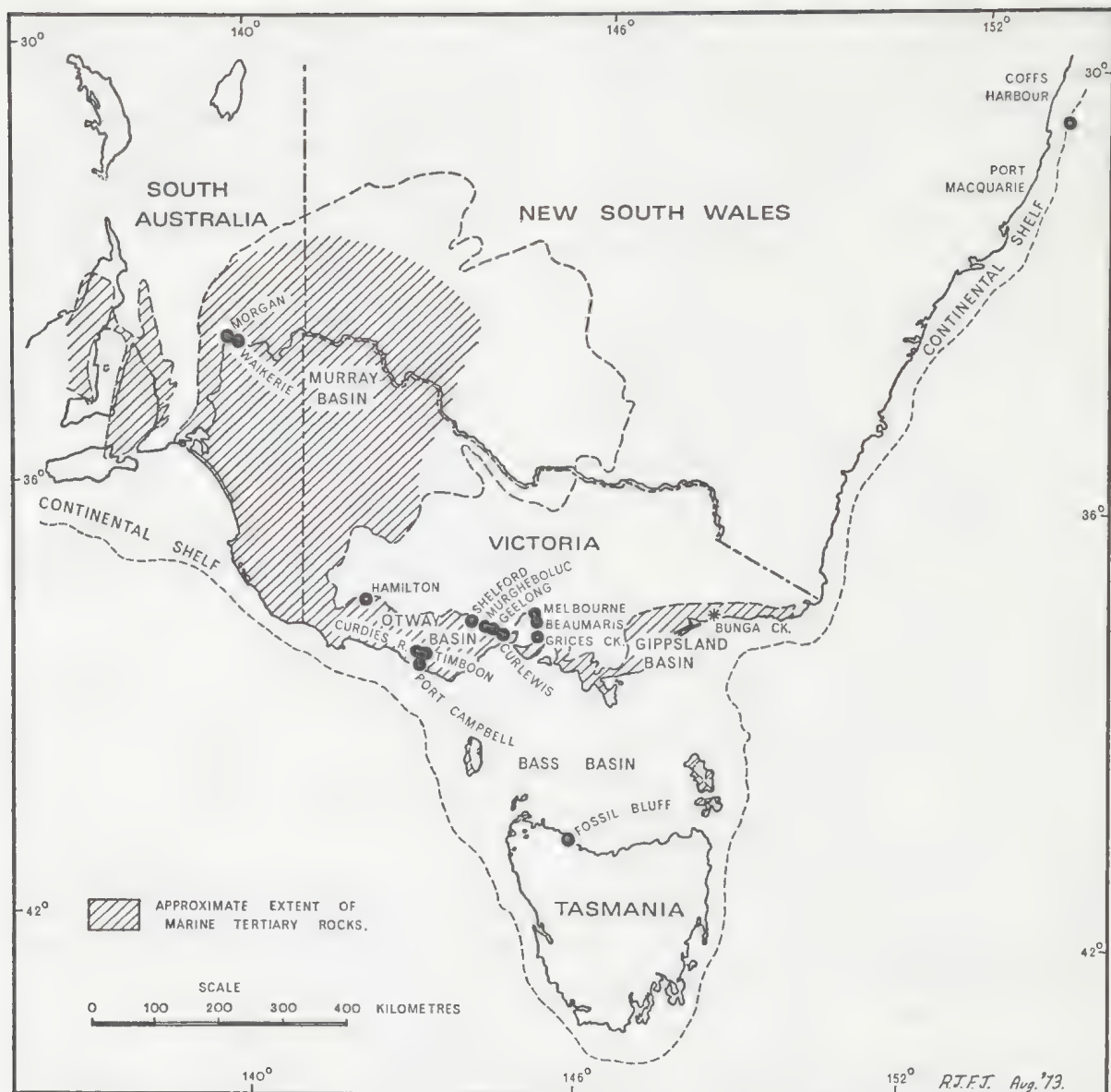


FIGURE 5

Locality map showing occurrences of fossil remains of *Ommatocarcinus* in southeastern Australia. ●, *Ommatocarcinus corioensis* (Cresswell). *, fragmentary remains tentatively identified as *Ommatocarcinus macgillivrayi* White.

limestone bed with *Hinnites corioensis* McCoy, Fyansford Clay, North Shore, Geelong, Victoria (Singleton, 1968). Bairnsdalian (Bowler, 1963), Middle Miocene.

Numerous remains are in remanié phosphatic nodules from the base of Moorabool Viaduct

Sands, Geelong area, Victoria. Localities include Murgheboluc, Batesford, Fyansford, Cowies Creek, North Shore and Western Beach at Geelong, the vicinity of Fenwick, and the sea coast near Curlewis (location of lectotype). The nodules are probably derived from underlying Miocene sediments.

Fragmentary remains not enclosed in nodules are reported by Kebble (1932) as occurring in phosphatic nodule bed (base of Moorabool Viaduct Sands) in the Geelong area. They are possibly from *in situ* in Moorabool Viaduct

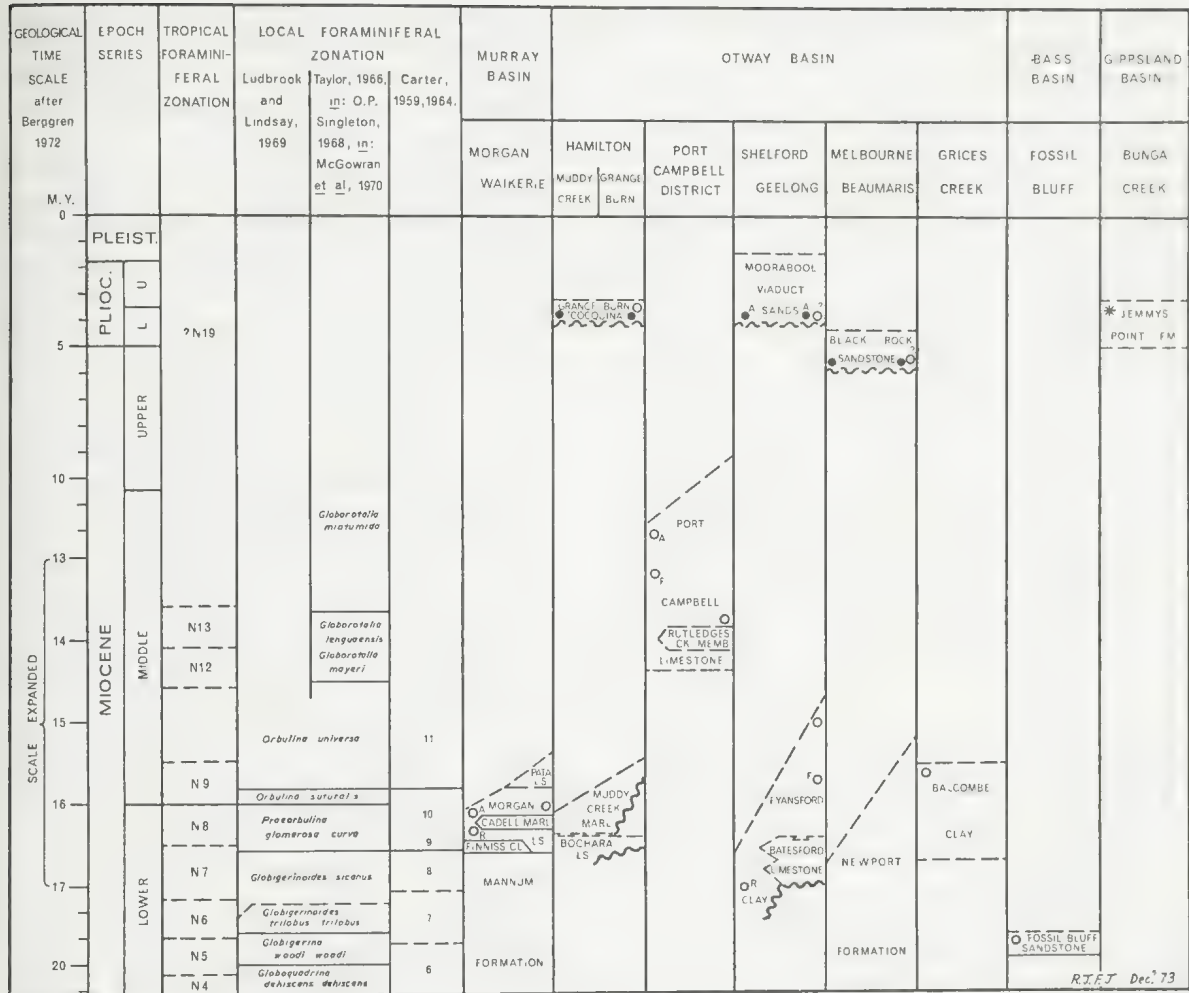


FIGURE 6

Stratigraphic distribution of *Ommatocarcinus* in southeastern Australia:

○: Occurrences of *O. corioensis* in situ (specimens from the Upper Miocene of the Geelong area and Beaumaris may possibly be remanié). ●: Occurrences of *O. corioensis* in remanié phosphatic nodules. *: Single fragmentary claw referred tentatively to *O. macgillivrayi*. A, specimens abundant. F, specimens frequent. R, specimens rare. Geological time scale after Berggren (1972).

Sands or derived from soft facies of underlying Miocene sediments.

Remains occur in remanié phosphatic nodules from the base of Black Rock Sandstone, Melbourne area, Victoria. Localities are a railway cutting at South Yarra, and the sea coast at Beaumaris. The Black Rock Sandstone is Cheltenhamian, late Miocene to ?early Pliocene.

Seven more or less fragmentary remains of uncertain stratigraphic level are known from the sea coast at Beaumaris. They are possibly from *in situ* in Black Rock Sandstone and Cheltenhamian, or remanié, derived from underlying Newport Formation of Lower to Middle Miocene age.

A pair of chelae came from Balcombe Clay, the downstream section of Grices Creek, 5 km N.N.E. of Mornington, Victoria. Faunal Unit 11 of Carter (1959, 1964), Bairnsdalian (Gostin, 1966), Middle Miocene.

Bass Basin

One specimen has been taken from Fossil Bluff Sandstone, Fossil Bluff, near Wynyard, northwest Tasmania. Faunal Unit 6 of Carter

(1959, 1964) according to Quilty (1972), Lower Miocene.

Continental slope off New South Wales

Two fragmentary remains in nodules are from the upper part of the continental slope off New South Wales (materials kindly donated by Professor C. C. von der Borch). One nodule was from 210 m depth at 30°41'S, 153°18'E off Coffs Harbour; the second from a depth of 247 to 274 m in the region of Coffs Harbour or Port Macquarie. The nodules are probably reworked concretions eroded from sediments of Miocene age (von der Borch, 1970).

Conclusions

The stratigraphic range of *O. corioensis* is from within the Lower Miocene to the Pliocene. The numbers of specimens taken *in situ* in different stratigraphic intervals suggests that the species was rare during most of the Lower Miocene, numerous or even abundant at different times in the late Lower and early Middle Miocene and mid Middle to ?Upper Miocene, and relatively uncommon in the late Upper Miocene and Pliocene. None of the possible Upper Miocene occurrences have been verified with certainty.

O. corioensis has not been recorded from the St. Vincent Basin of South Australia. The better known exposures of mid-Tertiary sediments in this basin predate the late Lower Miocene increase in abundance of the species.

Palaeoecology of *O. corioensis*

Mode of occurrence

Remains of *O. corioensis* found *in situ* are usually preserved in a life-like attitude with the dorsal aspect uppermost (Fig. 7A, B, Pl. 4, figs. 5a-d, Pl. 5, figs. 1a, 2a, 6 and 9). The fossils may either be remains of dead animals or moults, since the pleural sutures are invariably fractured. If they are moults the carapace has fallen back into place in the manner described by Schüfer (1951). It is considered more likely that most are remains of dead animals and that the sutures were weakened by post-mortem decalcification and broken due to compaction of the enclosing sediment. Almost all specimens are slightly crushed, some greatly so. The atti-

tude in which the crabs are preserved indicates that their appendages have been supported by the sediment enclosing them (Fig. 7B), and suggests that the animals were already buried at the time of death.

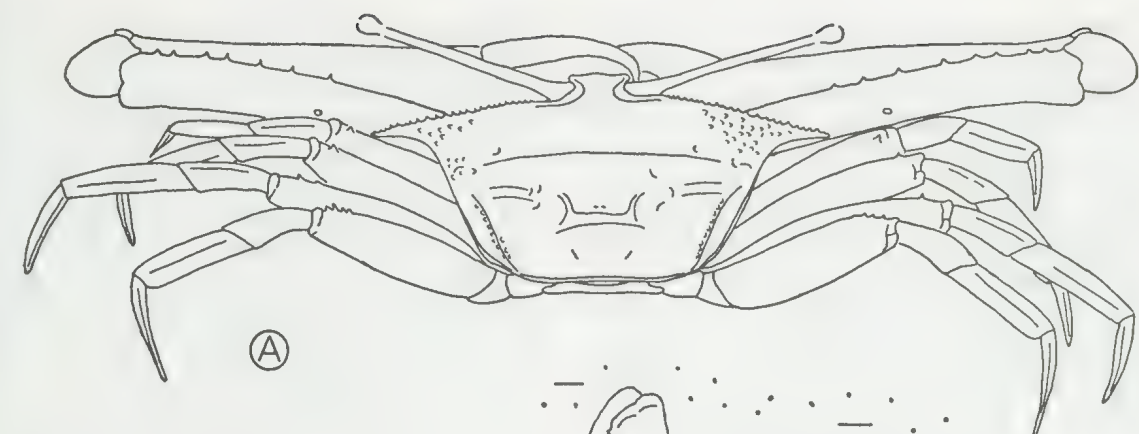
Hall (1905) suggested that the conditions of preservation of remains of *O. corioensis* occurring in the cliffs of the Port Campbell area indicated that the crabs were 'entombed in their burrows'. The writer has found specimens associated with fossil burrows weathering out of the flat bedding-plane erosion surfaces which form in the Port Campbell Limestone on the tops of these cliffs (Pl. 8, figs. 2 and 3). The burrows are usually sub-cylindrical structures 3-6 cm wide and lying more or less in the plane of the bedding. Frequently they form branching complexes with individual forks at intervals of 5 cm to 1 m apart (Fig. 7C and D, Pl. 8, figs. 1 and 5). Often the burrows are deeper than wide and have a layered infilling, the layers curving obliquely upwards towards the roof of the structure (Pl. 8, fig. 4); this layering may have resulted from the crab plastering material onto the bottom of the burrow. Other crabs are associated with more or less irregular structures which may represent an infilled funnel leading down to a burrow.

The burrows are clearly dwelling structures (*Wohnbauten* of Seilacher, 1953) which the animal maintained and occupied for a significant length of time, probably for protection. The burrows strikingly resemble those which Rice and Chapman (1971) describe for the extant, European *Goneplax rhomboides* (Linné) a crab closely related to *Ommatocarcinus*. The males of *Goneplax* have the chelipeds similarly

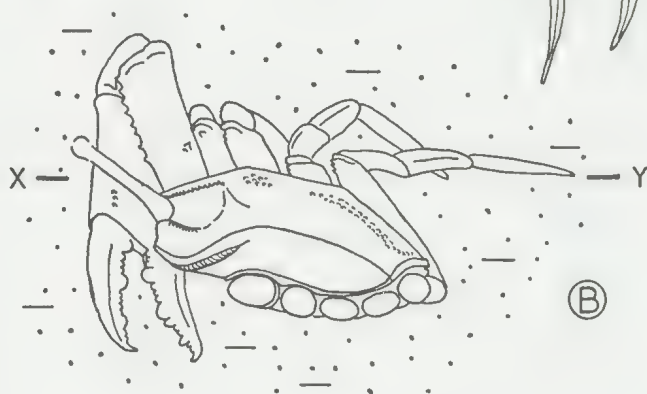
FIGURE 7

A-B: *Ommatocarcinus corioensis* (Cresswell); A, reconstruction of ♂ specimen N.M.V. P24721 in dorsal view, showing its life-like attitude as preserved in the sediment (cf. Pl. 5, fig. 1), x 11/12; B, partial reconstruction of crab in lateral view showing how its appendages were evidently supported by a level of sediment no lower than the line X, Y at the time of preservation, x 1½.

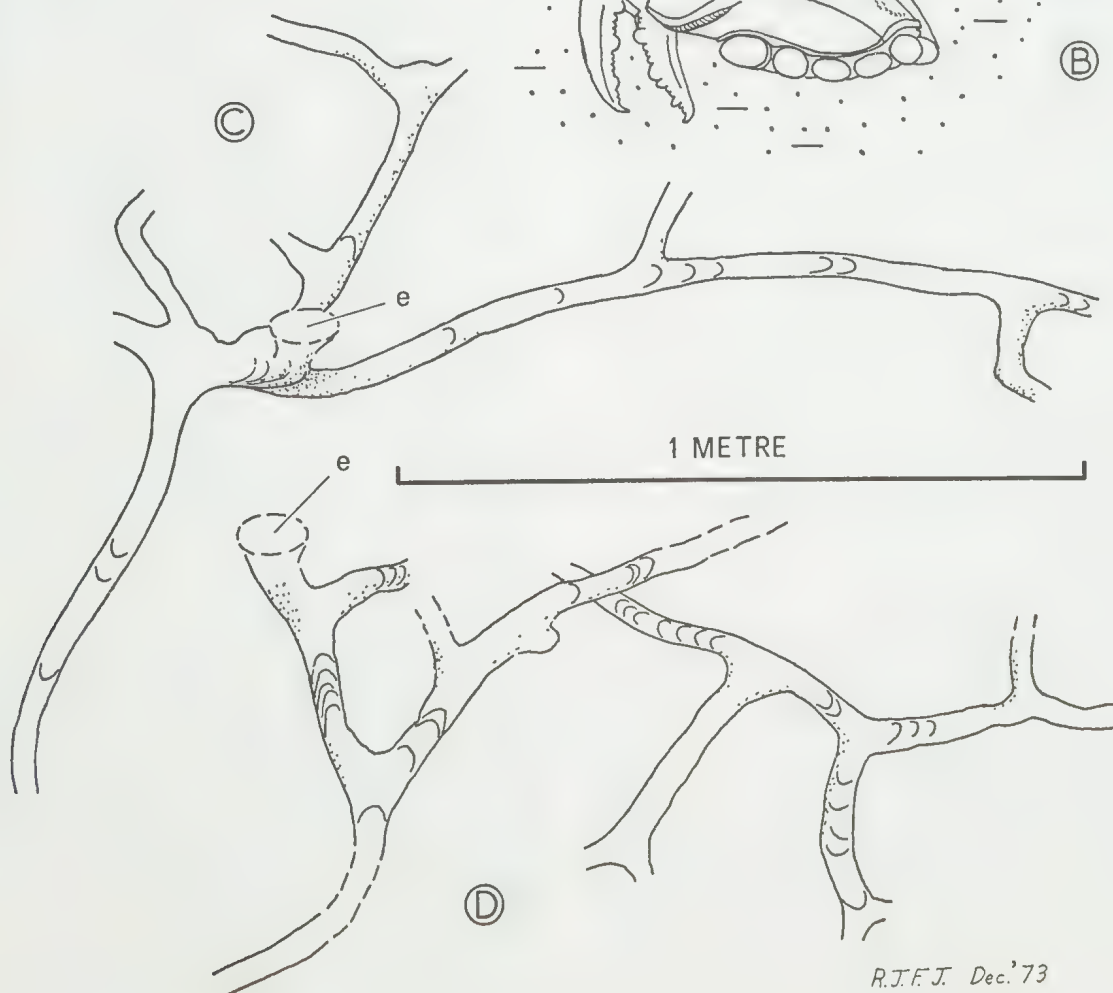
C-D: Burrow complexes attributed to *O. corioensis* and occurring in the Port Campbell Limestone at the mouth of the Sherbrook River near Port Campbell; c, assumed position of entrance funnel; complex illustrated in D also shown in Pl. 8, fig. 5.



(A)



(B)



(C)

(D)

elongated as in *Ommatocarcinus* and Rice and Chapman document the important function of the chelipeds in either pushing mud away from the crab or carrying mud during burrowing. It seems highly probable that the chelipeds of *Ommatocarcinus* are adapted to perform the same function. The elongate eyestalks of *Goneplax* fold laterally into trough-like orbits as in *Ommatocarcinus*, thus enabling the crab to move sideways along narrow passageways.

Very numerous remains of *O. corioensis* in the Port Campbell cliffs and at other localities do not show any relationship to obvious burrow structures. Possibly these animals died after digging down into, and burying themselves in loose sediment. Hence *O. corioensis* may have constructed semi-permanent burrows as well as being able to rapidly bury itself for protection when distant from a dwelling burrow.

Keble (1932) noted that collections of *O. corioensis* from *in situ* tend to have a preponderance of smaller individuals. This has been verified for the Port Campbell Limestone where individuals with the carapace only 9 mm wide may be found. The abundance of smaller individuals is suggestive of an approximation to a life-assemblage or biocoenose (see Boucot, 1953).

In all the collections at my disposal there is a notable inequality in the numbers of each sex; males are about ten times more numerous. This inequality may partly reflect preferential preservation of long clawed specimens in phosphatic concretions and nodules, but is not readily explicable for unphosphatized, non-remanié remains occurring *in situ*.

Life environments

O. corioensis is a relatively common fossil in the top 3 m interval of the upper member of the Morgan Limestone, 6 km south of Morgan. A count of 120 shells of the bivalve *Spondylus pseudoradula* McCoy occurring in a bed within this interval gave a ratio of about 1:5 for the number of articulated valves against disarticulated valves. Hence these beds appear to have been deposited in a relatively low-energy environment, but in water certainly shallower than wave base. The fauna of the interval suggests a shallow environment and

includes the brachiopod *Magellania macleani* (Tate), separated valves of *Ostrea* Linné, cirripedes (attached to shells), remains of the thalassinid decapods *Callianassa* Leach and *Ctenocheles*, the large benthonic foraminifera *Marginopora* Quoy and Gaimard, and small coralline algae. Some of the latter are grouped together in life orientation. In modern seas *Marginopora* is most common in very shallow water down to 27 m in depth (Adams, 1965). Coralline algae are mainly found at tide level to 30 m deep (Johnson, 1961). Hence at this locality *O. corioensis* probably lived in moderately active waters less than 30 m deep.

Bowler (1963) analysed the environment of deposition of the Fyansford Clay at North Shore, Geelong, another locality for *O. corioensis*. On the basis of the lithology, the sand clay ratio and the mineralogy of the sediments, he suggests that deposition occurred in 'very shallow' water which was alkaline and had a positive Eh.

The most abundant occurrence of *O. corioensis* known is in the Port Campbell Limestone, which Glenie (1971) characterizes as a transgressive, neritic, marine unit. Singleton (1968) suggests that this limestone was deposited in a quiet off-shore environment, but not pelagic, and considers that the relatively fine grained, bioclastic, lime sands composing it were washed in from shallow water. Thus the depth range of *O. corioensis* was probably not dissimilar to that of the living *O. macgillivrayi*, which is known from 'shoal water' to 80 m in Australian waters and down to 274 m off Japan.

Associated sediment type

All specimens, including those in phosphatic nodules, appear to have been originally fossilized in limy sediments. Of the specimens collected *in situ*, 76 per cent are in fine grained bioclastic limestones which have a high proportion of foraminiferal fragments, a little glauconite, and some silt. Thirteen per cent are enclosed by silty calcarenite or marl with other shelly fossils. Seven per cent have a matrix of calcareous siltstone; and four per cent are in calcarenites with some quartz sand. The two largest percentages given are disproportionately

high due to extensive collecting from large outcrops.

Selected examples of the matrix of different specimens had a silt-clay fraction ranging from 9 to 53 per cent of the rock by weight. Only a few grains of quartz sand were present. One calcarenite matrix contained five per cent by weight of fine to medium grained angular quartz sand and a little silt.

The general association of *O. corioensis* with relatively fine grained sediments almost certainly reflects its burrowing habits. A sediment fine enough for ready excavation but not so fine as to smother the crab or collapse readily seems to have been preferred. The apparent close association with limey sediments may be an artefact of the nature of the materials being chiefly deposited; quartz rich sands of similar age are rare in southern Australia.

Isotopic temperatures and relative abundance

Dorman (1966) presents numerous relatively recent results of oxygen isotope temperature measurements made on shelly fossils, mainly bivalves, collected from the Tertiary rocks of southern Victoria. A comparison between some of the better dated items of this data and the numbers of *O. corioensis* found in different stratigraphic intervals is shown in Figure 8. The crab is a rather rare species during most of the Lower Miocene, but becomes abundant during the latest Lower Miocene and earliest Middle Miocene. It is again abundant during the later part of the Middle Miocene (and possibly early Upper Miocene). There is little or no evidence to relate these times of abundance with the relatively high isotopic temperatures of 23-25°C. recorded in the late Lower and Middle Miocene. Rather, the crabs seem to have been common during cooler intervals with isotopic temperatures of the order of 14-17°C. Tropical crab genera, *Calappilia* A. Milne Edwards and a tropical section of *Nucia* Leach, appear in the southern Australian Tertiary during the high temperature interval of the late Lower Miocene (Jenkins, 1972), and ingressions of the warm water foraminifera *Lepidocyclina* Gümbel, *Cycloclypeus* Carpenter and *Marginopora* at this time (Carter, 1964; Lindsay, 1969, 1970; Lindsay and Giles, 1973)

are clearly related to the same event (Fig. 8). A distinctly later ingressions of the warm water, foraminiferal genus *Flosculinella* Schubert and Richarz is linked to the appearance of *Orbulina suturalis* Bronnimann in the Adelaide Plains Sub-Basin of the Port Vincent Basin (Lindsay, 1969). As later members of the *Orbulina* bioseries occur only rarely in the Adelaide Plains Sub-Basin (Lindsay, 1969, p. 38), this dating of the *Flosculinella* ingressions cannot be regarded as sharply fixed. It thus seems plausible that the ingressions of this genus is related to the high-temperature event during the *Orbulina universa* Zone.

The possible *in situ* occurrences of *O. corioensis* in the latest Miocene (Beamaris and Geelong district) and its better documented occurrences in the Pliocene of Grange Burn, Hamilton, seemingly relate to isotopic temperatures of 13-18°C. The living *O. macgillivrayi* is known along the eastern Australian coast between 24°S and 34°S, where sea-water temperatures between 0 and 100 m depth range from about 14-17°C. to above 27°C.

As well as to the direct influence of climate, the abundance of *O. corioensis* is probably also linked to its burrowing habits and sediment facies. For most of the Lower Miocene the marine sediments of the Murray Basin and western parts of the Otway Basin were chiefly rather coarse grained bioclastic limestones, while similar limestones and fossiliferous clays predominated in the central and eastern parts of the Otway Basin. Deposition of silty limestones, calcareous silts and silty marls became widespread in the late Lower Miocene (e.g. the Morgan Limestone, Fyansford Clay and Balcombe Clay) and it is in these sediments that *O. corioensis* first becomes numerous. This phase of sedimentation was evidently a secondary result of climate; the influx of silt from erosion of a mature extra-basinal topography which underwent deep chemical weathering during the preceding time of near-tropical climate, coupled with the continuing high productivity of shelly organisms in the warm, shallow seas. The Port Campbell Limestone was a localized, relatively fine-grained off-shore facies which was obviously highly suited to the life habits of the crab.

FIGURE 8

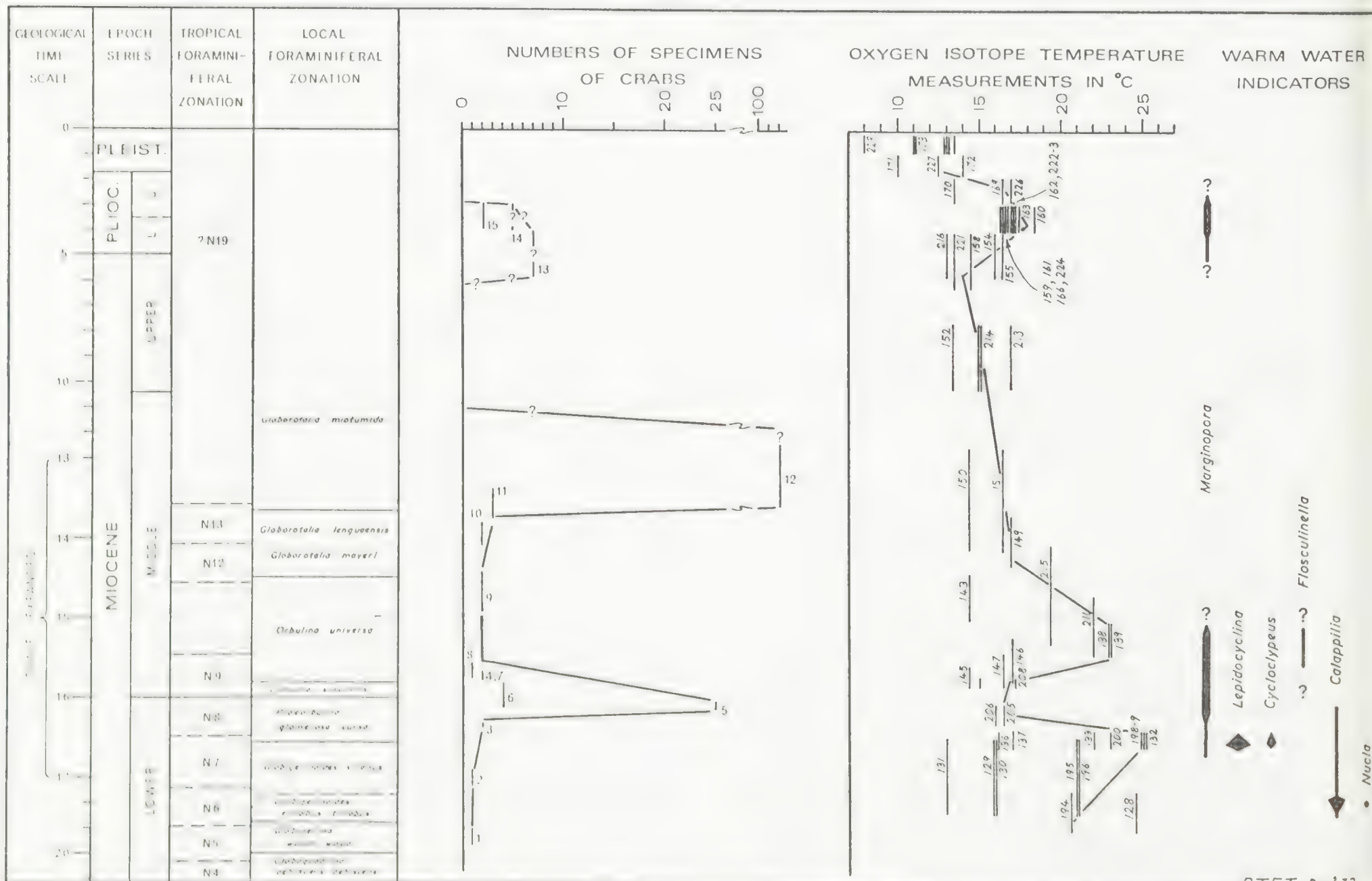
Comparison between the numbers of specimens of *Ommatocarcinus corioensis* found *in situ* at different localities representing various ages (occurrences numbered 1-15) and oxygen isotope temperature data for the region of southern Victoria. The correlation of Lower and Middle Miocene data is based largely on planktonic foraminifera; correlations for later times based largely on mollusca. The isotope temperature measurements are selected from data presented by Dorman (1966); his numbering of each item is indicated. The fossil crab localities are as follows: 1, Fossil Bluff; 2, Amphitheatre, Shelford; 3, lower member of Morgan Limestone at type section near Morgan; 4, section 2B Murgheboluc; 5, upper member of Morgan Limestone at type section near Morgan; 6, Waikerie; 7, Murgheboluc (specimens probably more numerous than data suggests); 8, Grices Creek; 9, North Shore, Geelong; 10, Port Campbell Limestone, apparently not far above Rutledges Creek Member, Amphitheatre near Port Campbell; 11, same locality as 10, higher in cliff; 12, Port Campbell Limestone, cliff tops in Port Campbell area; 13, Beaumaris (specimens possibly remanié); 14, Geelong area (specimens possibly remanié); 15, Grange Burn, near Hamilton.

Distribution and evolution of *Ommatocarcinus*

The known range of the genus is from the Middle Eocene to the present. *O. zariquieyi*, the oldest known species, occurs in the Middle Eocene of north eastern Spain. Presumably the genus migrated along the Tethys to the Indo-Pacific region, where *O. corioensis* and *O. arenicola* are the earliest known forms. *O. corioensis* is first recorded from early Miocene rocks in Tasmania; *O. arenicola* occurs in the Lower Miocene of the South Island of New Zealand.

With the exception of *O. orientalis*, the modern representatives of the genus are restricted to the sub-tropical and temperate climatic zones. The fossil species are found in latitudes similar to those inhabited by the recent forms.

As is suggested earlier in this paper the



occurrence of *O. corioensis* in southeastern Australia probably reflects water temperatures somewhat warmer than at present. It extended 4° to 7° further south than the known range of the living *O. macgillivrayi*, and is most abundant during the latest Lower and early Middle Miocene, and late Middle Miocene, when oxygen isotope temperature measurements on other shelly fossils give values of 14–17°C. Its abundance is also linked to phases of deposition of soft sediments which enabled it to pursue its burrowing habits.

Water temperature apparently influences the modern distribution of *O. macgillivrayi* near Japan (Yokoya, 1933). Where the warm Kuroshio Current touches on the east coast of Japan the crab is found as far north as the Bōsō Peninsula (latitude approximately 35°N). West of Japan the warm northward current meets the cooler water of the Japan Sea and *O. macgillivrayi* is known only as far north as Nagasaki (latitude 32°48'N). Transport of pelagic larvae by an eastward current probably enabled *O. huttoni* to reach the Chatham Islands from New Zealand (Dell, 1968). *Ommatocarcinus* is not recorded from the Americas. The Atlantic and Pacific appear to have formed eastern and western barriers respectively.

Members of *Ommatocarcinus* strikingly resemble species of *Goneplax*, not only in the general features of their morphology such as the shape of the carapace and the elongate eyestalks and chelipeds, but also apparently in behaviour, notably the habit of burrowing. Glaessner (1960) indicated the close similarity between the outline of the carapace of *O. arenicola* and the living *Goneplax rhomboides*, the type species of *Goneplax*. The resemblance is at least as great between *O. arenicola* and *Goneplax gulderi* Brachmayer from the Tortonian (Upper Miocene) of Austria. *Goneplax* is not recorded earlier than the Middle Miocene (*Goneplax* cf. *sacci* Crema, Glaessner from the Helvetian of Austria). Thus it is suggested that *Goneplax* evolved from *Ommatocarcinus* (Fig. 9).

In the evolutionary lineages within *Ommatocarcinus*, tentatively indicated in the same figure, several trends are apparent. The front

is rostrate in the oldest known species, but anteriorly truncated and with deep inner-orbital notches in all later forms. The change in form of the anterior margin of the front appears to be an adaptation to allow greater freedom of movement of the antennules; the anterior margin is gently concave above the antennules in *O. corioensis*, *O. huttoni* and *O. orientalis*, while in *O. macgillivrayi* distinct antennular notches are present. The inner-orbital notches narrow the front and probably facilitate erection of the eyestalks. It is notable that the basal segment of the eyestalks is concealed below the front in *O. corioensis* (and apparently in *O. zariquieyi*), but is exposed in all the extant species. In *Goneplax* the evolution of the front has evidently been more conservative and the inner-orbital notches are relatively shallow.

Another tendency in *Ommatocarcinus* is for reduction of the male abdomen. In *O. huttoni*, *O. orientalis* and *O. macgillivrayi* the basal segments of the abdomen are variously reduced in width. The third, fourth and fifth segments are fused in *O. zariquieyi* and *O. huttoni*.

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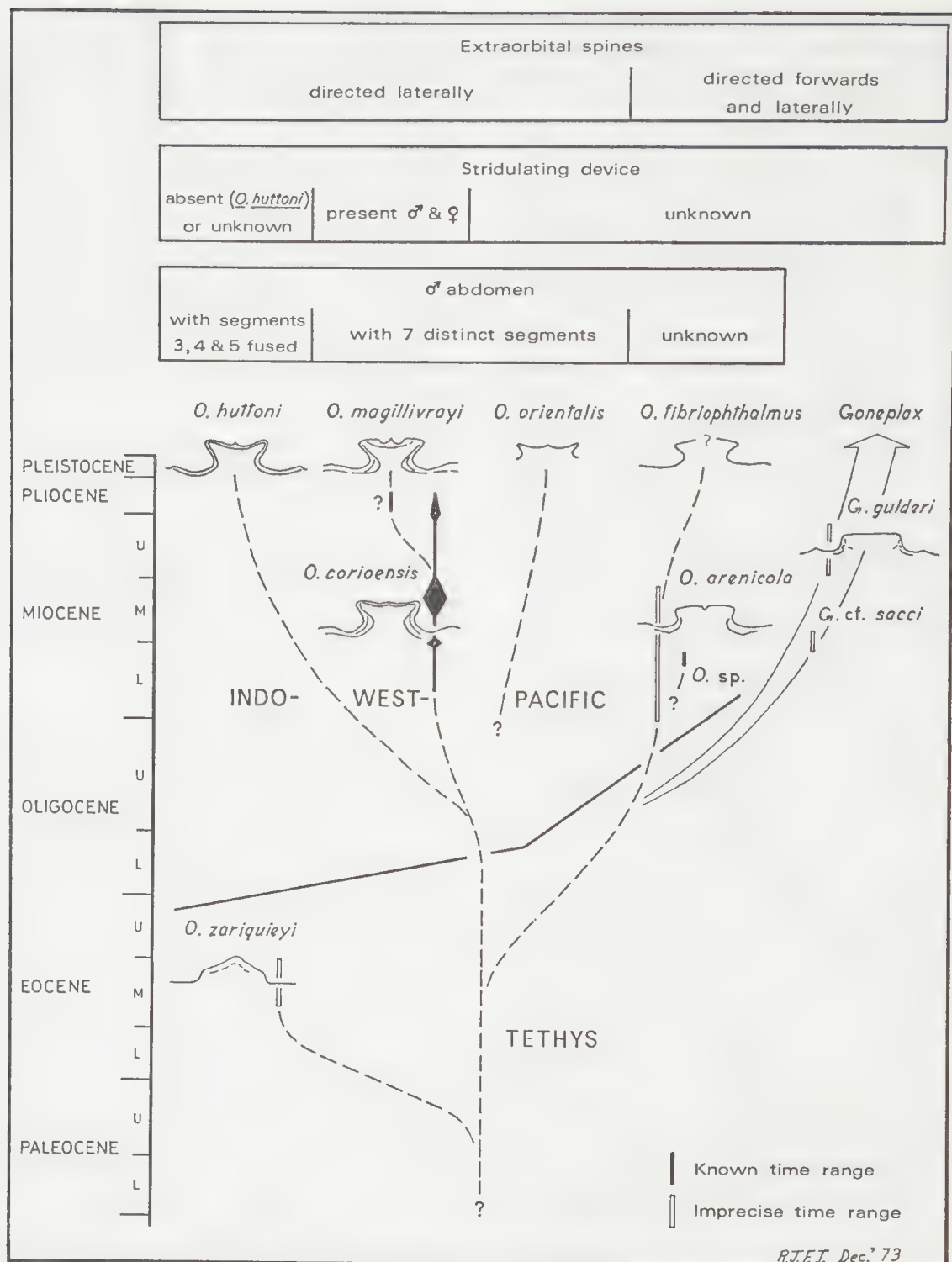


FIGURE 9

Evolutionary lineages within *Ommatocarcinus* and suggested origin of *Goneplax*. The front of most

species in illustrated (*O. zariqueyi* after Vía, 1959; *O. arenicola* after Glaessner, 1960; *O. orientalis* after Tesch, 1918; *O. fibriophthalmus* after Yokoya, 1933; *G. gulderi* after Bachmayer, 1953).

comparison. Dr R. R. Lamacroft, C.S.I.R.O., programmed data for the regression analyses. The project was supported by a C.S.I.R.O. Junior Postgraduate Studentship.

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Explanation of Plates

PLATE 4

Ommatocarcinus corioensis (Creswell)

- Fig. 1. Lectotype, dorsal view. In a remanié phosphatic nodule from (the base of the Moorabool Viaduct Sands) Curlewis, Victoria: N.M.V. P7665a; x 1½.
- Fig. 2. Carapace, dorsal view. The hind part of the carapace is preserved as an internal mould which shows muscle attachment areas adjacent to the anterior of the intestinal region. From (the Port Campbell Limestone) Curdies River lime works, Victoria: N.M.V. P26118; x 1½.
- Fig. 3. Internal mould of carapace, dorsal view. Areas of muscle attachment are indicated by a raised or reticulate ornamentation. In a remanié phosphatic nodule from the base of the Moorabool Viaduct Sands, Batesford, Victoria: A.U. F17214; x 1½.
- Fig. 4. Front, dorsal view. From (the Port Campbell Limestone) Two Mile Beach, near Port Campbell, Victoria: hypotype of Hall (1905), ♀, N.M.V. P7668; x 3.
- Fig. 5a-d. Mature male. From the Port Campbell Limestone, notch east of the Amphitheatre, Port Campbell: N.M.V. P24719.
- a, dorsal view: x 1.
- b, anterior view: x 1.
- c, anterior view, enlarged. S, pterygostomial stridulating ridge; P, plectrum on cheliped merus. The pleural suture is broken: x 2.
- d, ventral or external view of hands: x 1.
- Fig. 6. Stridulating ridge on anterior of pterygostomial region. In a remanié phosphatic nodule from the base of the Moorabool

Viaduct Sands, railway cutting at Cowies Creek, near Geelong, Victoria: A.U. F17216; x 3.

Fig. 7. Right chela of mature male. From near the top of the upper member of the Morgan Limestone at the type section, 6 km south of Morgan, South Australia: A.U. F17218; x 1.

Fig. 8. Inner sides of left fingers and right chela. From the Balcombe Clay, downstream section at Grices Creek, near Mornington, Victoria: N.M.V. P26050; x 1.

PLATE 5

***Ommatocarcinus corioensis* (Cresswell)**

Fig. 1a,b. Mature male. From the Port Campbell Limestone, Gravel Point, near Port Campbell: N.M.V. P24721.
a, dorsal view; x 1.
b, posterior view showing the first three abdominal segments; x 1.

Fig. 2a,b. Mature male. From (the Port Campbell Limestone) Two Mile Beach, near Port Campbell: hypotype of Hall (1905), N.M.V. P7667.
a, ventral view; x 1.
b, propodi of first two legs, showing ventral lines of pits; x 2.

Fig. 3. Sub-frontal region and epistome, anterior view. From the Port Campbell Limestone, top of cliffs at Point Hesse, west of Port Campbell: ♂, N.M.V. P25989; x 3.

Fig. 4a,b. Moderate sized female. In a remanié phosphate nodule from the base of the Moorabool Viaduct Sands, 'Coghills', near Geelong: A.U. F17221.

a, third maxillipeds, ventral view. The inner margin of the right ischium and outer margin of the left ischium are damaged; x 4.

b, sternum and abdomen, ventral view: x 1½.

Fig. 5. Sternum and abdomen of male. In a remanié phosphatic nodule from the base of the Moorabool Viaduct Sands, 'Rugby Pk.', near Fenwick, western Bellarine Peninsula, Victoria: A.U. F17219; x 1½.

Fig. 6. Moderate sized female, dorsal view. From (the Fyansford Clay) section 2B, Parish of Murgheboluc, Victoria, N.M.V. P25987; x 1.

Fig. 7. Merus of cheliped, ventral view, showing spines on the anterior and ventral margins. From (the Port Campbell Limestone) Two Mile Beach, near Port Campbell: ♀, N.M.V. P25988; x 2.

Fig. 8. Ventral view of small individual in a concretion from the Grange Burn Coquina, Forsyth's Bank, Grange Burn, near Hamilton, Victoria: N.M.V. P24689; x 2.

Fig. 9. Dorsal view of specimen from the Fossil Bluff Sandstone, Fossil Bluff, near Wynyard, Tasmania: T.U. 55357; x 1.

Fig. 10. Carapace of mature male, dorsal view. From near the top of the upper member of the Morgan Limestone at the type section, 6 km south of Morgan. A.U. F17217; x 1.

***Ommatocarcinus macgillivrayi* White**

Fig. 11. Left cheliped palm and fragment of carpus tentatively referred to *O. macgillivrayi*. From the upper shell bed in the Jemmys Point Formation, road cutting on the west side of Bunga Creek, near Lakes Entrance, Victoria: N.M.V. P24686; x 1.

PLATE 6

***Ommatocarcinus macgillivrayi* White**

Fig. 1. Holotype. From Port Curtis, Queensland. Photographs by courtesy of the British Museum of Natural History: ♂, 50-11, (Brit. Mus. dried coll.). Outer side of chelae at top, inner side of chelae immediately below; carapace and appendages in dorsal view.

Fig. 2. Carapace of mature male, dorsal view. From near Sydney, New South Wales: A.M. P1147; x 1.

Fig. 3. Carapace of male. Sub-fossil, from dredgings at Luggage Point, mouth of Brisbane River, Morton Bay, Queensland: Q.M. F5624; x 1.

PLATE 7

***Ommatocarcinus macgillivrayi* White**

Fig. 1. Female, ventral view. From Sow and Pigs Shoal, Port Jackson, New South Wales: A.M. P10090; x 4/5.

Fig. 2a-e. Mature male. From near Sydney, New South Wales: A.M. P1147.

a, front, anterior view; x 2.

b, third maxillipeds, antennules and antennae, ventral view; x 2½.

c, pterygostomial stridulating ridge (S) and plectrum (P) on cheliped merus, anterior view; x 2.

d, sternum and abdomen, ventral view: x 1½.

e, basal abdominal segments, posterior view. The carapace is slightly raised to expose the first segment; x 1½.

***Ommatocarcinus huttoni* Filhol**

Fig. 3a-c. Male, from off Greymouth Bar, South Island of New Zealand: D.M. Cr1765.

a, carapace, dorsal view; x 2.

b, right (upper) and left chelae, inner surfaces shown; x 1½.

c, sternum and abdomen, ventral view; x 2.

Fig. 4a,b. Female, from Cook Strait, New Zealand: D.M. Cr1171.

a, front and epistome, anterior view; x 4.

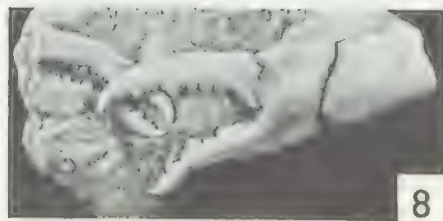
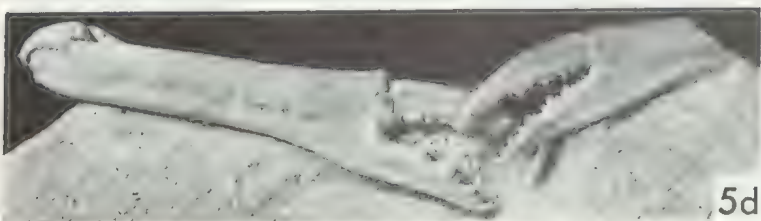
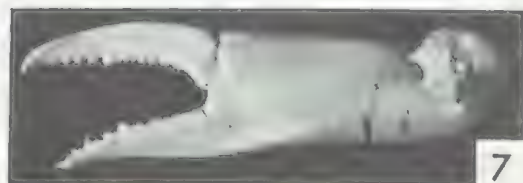
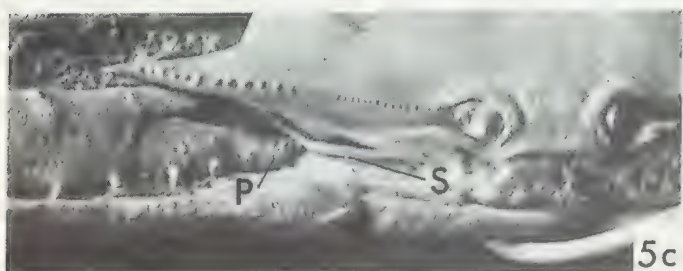
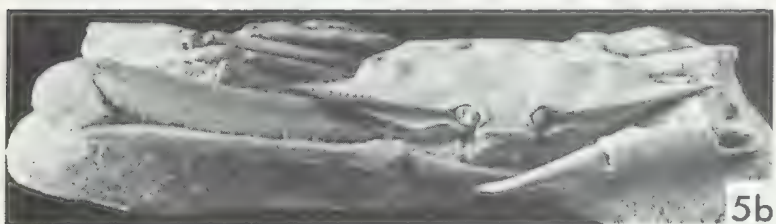
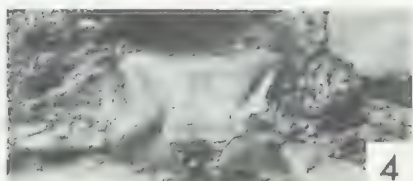
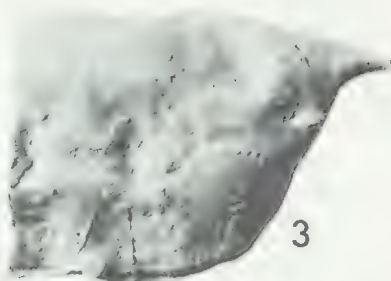
b, third maxillipeds and anterior part of pterygostomial region, ventral view; x 4.

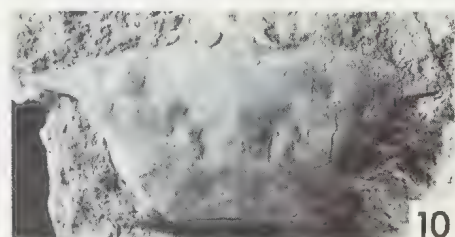
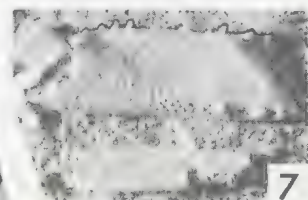
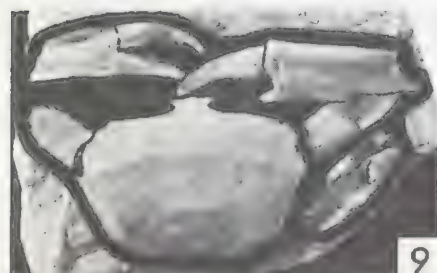
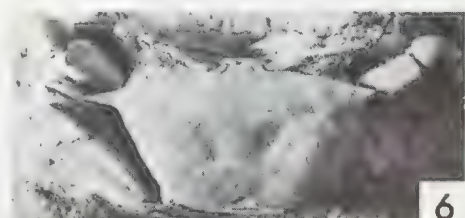
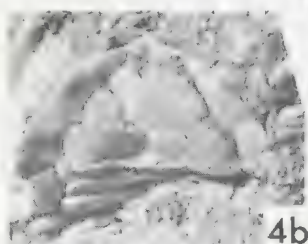
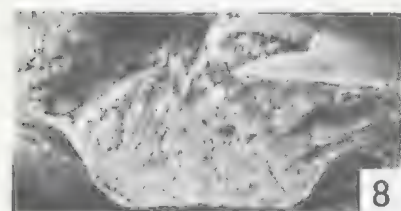
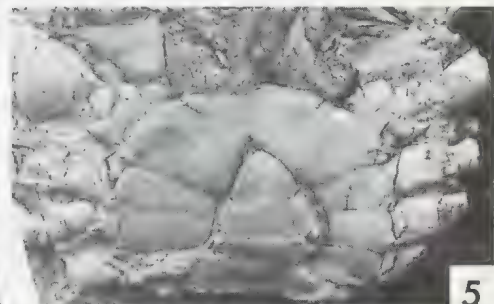
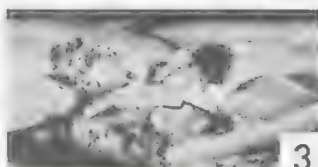
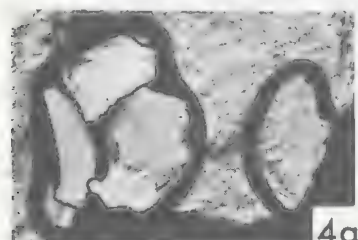
PLATE 8

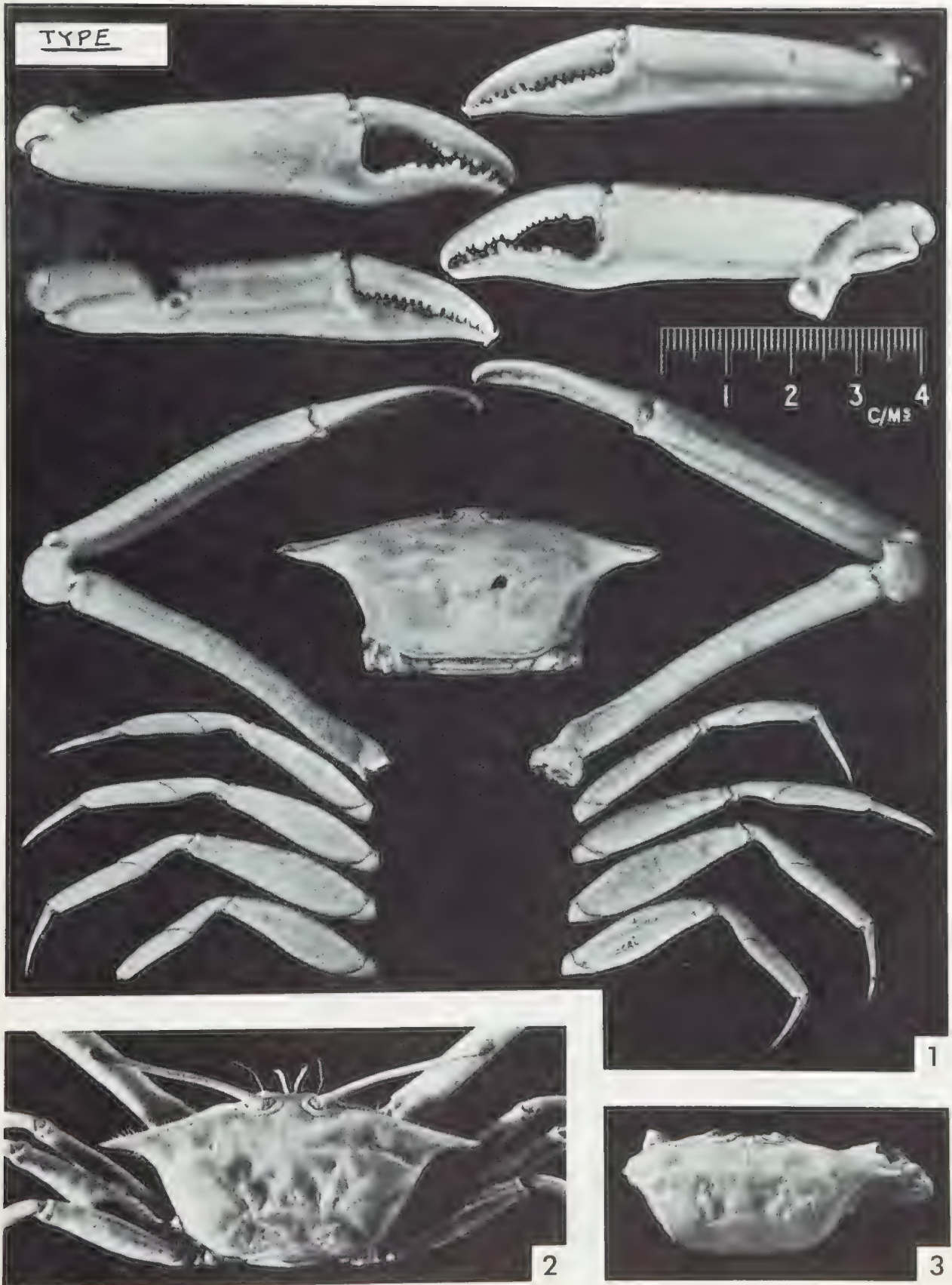
Burrows attributed to *Ommatocarcinus corioensis* (Cresswell) in the Port Campbell Limestone in the sea cliffs of the Port Campbell area, Victoria.

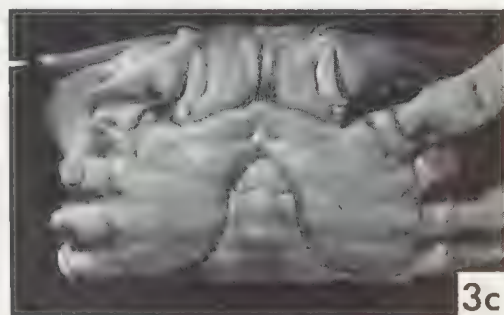
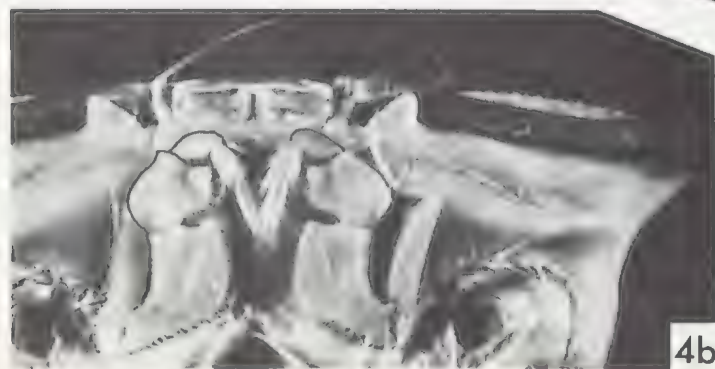
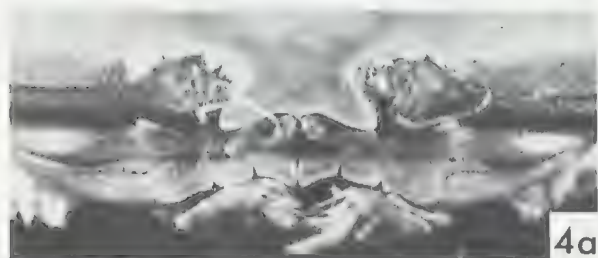
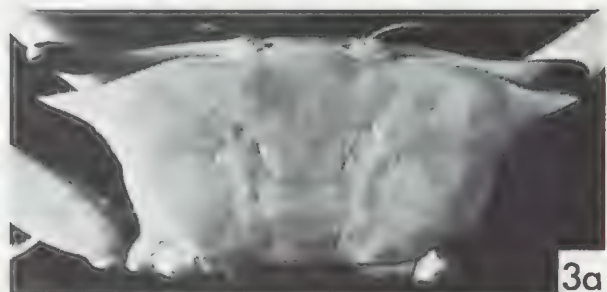
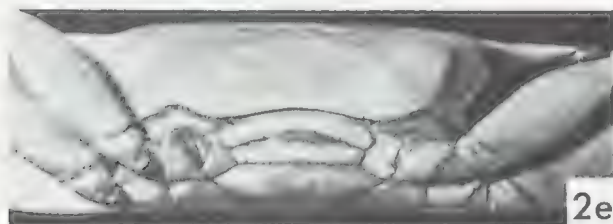
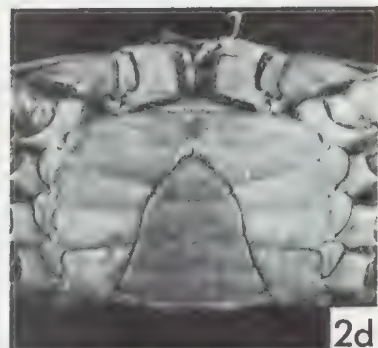
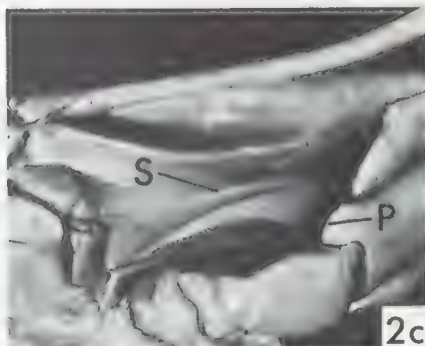
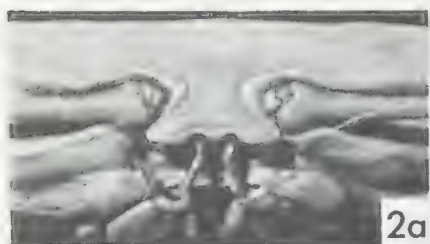
Fig. 1. Burrow complex weathering out of the bedding-plane erosion surface at the top of London Bridge, W. of Port Campbell. The hammer is 32 cm long.

- Fig. 2. Specimen of *O. corioensis* (near pen-top) preserved seemingly at the end of its burrow. Erosion surface at the top of Gravel Point, E. of Port Campbell. The pen-top is 6 cm long.
- Fig. 3. Specimen of *O. corioensis* associated with a burrow complex weathering out of a bedding plane erosion surface on a cliff top near the mouth of the Sherbrook River, E. of Port Campbell.
- Fig. 4. Lateral view of burrow infilling showing the shallowly oblique, gently curved lamination which is a frequent feature. Top of London Bridge. Bar scale equivalent to 10 cm.
- Fig. 5. Burrow complex weathering out of a bedding-plane erosion surface on a cliff top near the mouth of the Sherbrook River. E, probable remnants of burrow entrance funnel.











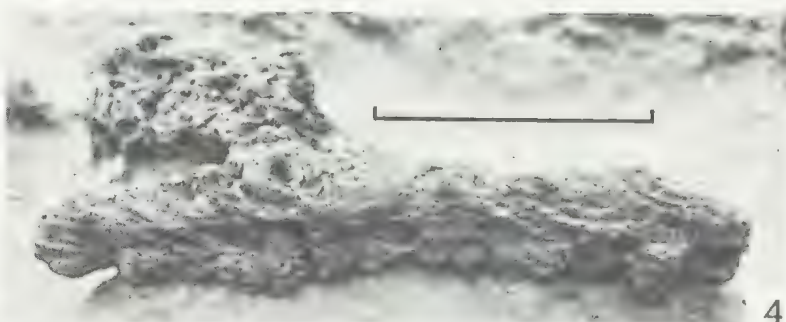
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5

ANTARCTIC DISPERSAL ROUTES, WANDERING CONTINENTS, AND THE ORIGIN OF AUSTRALIA'S NON-PASSERIFORM AVIFAUNA

By PAT VICKERS RICH *

* The Museum, Texas Tech University, Lubbock, Texas, U.S.A. 79409; present temporary address, The National Museum of Victoria, Russell Street, Melbourne, Victoria.

Introduction

In 1858, P. L. Sclater recognized Australia on the basis of its living avifauna, as a unique biogeographic unit, distinct from the Oriental fauna that characterized the Asian mainland. These two faunas complexly intermingle on the islands of the Indonesian archipelago, a situation reflected not only by the birds but by other vertebrate and invertebrate groups as well. A. R. Wallace in a number of papers (1863, 1869, 1876) initially described the avifaunas he encountered in this transitional zone; his work was followed by numerous refinements (Stresemann, 1927-34, 1939-41; Rensch, 1931) culminating with those which led Mayr (1941, 1944a-b, 1945a-b, 1972) to conclude that the major part of Australia's avifauna was derived from Southeast Asia. Although Darlington (1957) agreed with this thesis and Gentili (1949) hinted at a dual origin, Serventy (1972, 1973) was the first to seriously consider multiple geographic origins of the Australian avifauna in light of the accumulating geological evidence suggestive of dynamic, not static, relationships of the continents during the Mesozoic and Cenozoic. Australia had not always been a neighbour of Asia. Serventy concluded, however, that excepting a few Australian families which might have used an Antarctic dispersal route, Mayr was correct in assuming that Southeast Asia had spawned most of the Australasian avifauna. Cracraft (1972, 1973) strongly supported an austral dispersal route for the ratites, megapodes, and possibly some parrots and suboscine passeriforms but otherwise subscribed to the thesis of northern origin for most other avian groups.

In the following paper, I wish to investigate the initial assumptions and the reasoning that have been used in previous studies to determine the source area for each of the Australian non-

passeriform families. In this way, I hope to clarify the certainties and uncertainties that accompany such determinations for each family, and to estimate which dispersal route (Antarctic or Indomalaysian) seems most probable for initial dispersal of each non-passeriform family between Australia and the remaining world. In order to evaluate the availability of the two routes for avian dispersal throughout the Mesozoic and Cenozoic, I have summarized: (1) data regarding the timing of break-up and separation of those continental plates closely associated with Australia during that time period; (2) paleoclimatological data available for the Antarctic and Indomalaysian dispersal routes, as well as for Australia during post-Paleozoic time; and (3) data available on phylogenetic relationships, world-wide diversity, endemism, distribution, and palaeontological record of all the non-passeriform avian families having a Cenozoic record in Australia.

Dispersal Routes To and From Australia

Geological Evidence

Antarctic Dispersal Route (Operative, Mesozoic and early Cenozoic)

Geophysical data collected primarily in the last decade strongly support the idea that a southern dispersal route between Australia and certain other Gondwana continents was present during much of the Mesozoic, and between Australia and some southern continents as late as the early Tertiary (Allan, 1969; Creer, 1970; Francheteau and Sclater, 1969; Smith and Hallam, 1970; and others). Such a route was most likely of an archipelagic nature (similar to the linkage between Asia and Australia today) as geologic data suggest that complete terrestrial continuity probably has not existed between South America, West

Antarctica, East Antarctica,¹ and New Zealand (Tedford, 1973a; Jardine and McKenzie, 1972) during the mid to late Mesozoic and Cenozoic.

Time of the break-up of the many continental segments, originally part of Gondwanaland, can be estimated by using several types

¹ Present-day Antarctica can no longer be considered a single, terrestrially continuous unit, but is instead composed of at least two segments, East and West Antarctica, each with a distinct geologic history (Hamilton, 1964, 1967; Dalziel and Elliot, 1971, 1973; Elliot, 1972). At present West Antarctica is comprised of a number of islands separated from the continental East Antarctica by basins with sub-sea level depths.

of geologic evidence. Despite the controversies that still attend the Africa-Madagascar, Madagascar-India, Africa-India, Australia-India, East-West Antarctica continental pairs, general agreement exists among most supporters of plate tectonic theory on the time of fragmentation of many of Gondwanaland's several segments. Such fragmentation did not occur simultaneously, however, and original rupture between continent-pairs may have begun long before actual terrestrial continuity between land masses was lost (e.g. East Africa at present). Thus, a distinction needs to be made between evidence indicating initial rifting or break-up (B in Table 1), and that indicative of active

TABLE 1

Evidence available for timing the break-up and dispersal of Gondwanaland during the Mesozoic and Cenozoic (see Figure 1 for summary). B, break-up occurring (involving displacements of less than 100 km.); S, large-scale separation of continental masses underway.

<i>Continental Pair</i>		<i>Time of Break-up/Dispersal</i>	<i>Evidence</i>
1. SOUTH AMERICA-AFRICA	S	Post-Triassic to mid-Cretaceous (7, 13, 14, 17, 37, 38)	Polar wander curves.
	B	Aptian (27, 39)	Salt deposits in coastal West Africa and coastal Brazil.
	B	106-136 m.y. (late Jurassic-early Cretaceous) (7, 8)	Occurrence of massive tholeiitic basalt flows dated by K/A method on both sides of Atlantic; Serra Geral Fm. of Brazil; Kaoko volcanics of Southwest Africa; Lupata volcanics of Africa.
	S	70-75 m.y. (26, 29, 46)	Magnetic banding (oldest anomaly, 31).
	B	Post early Cretaceous (10)	Non-marine ostracod faunas virtually identical (at specific level) in Brazil and West Africa.
	S	Albian (mid-Cretaceous) (10, 18, 28)	Fully marine conditions indicated by sediments over broad areas on either side of South Atlantic.
2. SOUTH AMERICA-WEST ANTARCTICA (probably archipelagic during Jurassic to recent)	S	Late Turonian (12, 27, 28)	Fully marine conditions along western Africa. Ammonite faunas of North and South Atlantic similar.
	S	> 20-25 m.y. but > late Mesozoic (22)	Magnetic banding in the Drake Passage for minimum date; similarity of tectonostratigraphic provinces until end of Andean Orogeny (late Cretaceous-early Tertiary) for maximum date.
	S	Post-Cretaceous (24)	Paleomagnetism of volcanics and intrusives on Antarctic Peninsula indicate major bending of Peninsula occurred post-Cretaceous.
3. WEST ANTARCTICA-NEW ZEALAND (probably archipelagic, Jurassic to Recent)	S	80 m.y. (4, 5, 23, 26) (late Cretaceous)	Magnetic banding between Campbell Plateau and West Antarctica; oldest anomaly, 32.

<i>Continental Pair</i>	<i>Time of Break-up/Dispersal</i>	<i>Evidence</i>
	S 78 m.y. (19) (late Cretaceous)	Beginning of activity on Endeavour Fault (fault active between 47-78 m.y.).
	B Mid-Jurassic (3, 10)	Volcanics. Tasmanian dolerites, Ferrar dolerites (Antarctica).
4. EAST ANTARCTICA-AUSTRALIA (probably archipelagic Jurassic to Recent)	S Mid-Cretaceous-Tertiary (3, 13)	Polar wander curves.
	S 45-50 m.y. (1, 2, 4, 6, 10, 14, 16, 19, 26)	Magnetic banding between Australia and East Antarctica; oldest anomaly, 18.
	S Mid-late Eocene (1, 9, 10, 30)	Marine transgression in southern Australia; open marine limestones.
	S Late Oligocene (33, 36)	Erosional unconformity (marine) evidencing establishment of circum-Antarctic current.
	B Mid-Jurassic (42)	Dolerites in Tasmania and East Antarctica.
	B Late Jurassic to Cenomanian (43)	Rifting in southern Australia.
5. EAST ANTARCTICA-AFRICA	B Triassic-Jurassic (11)	Onset of rifting, southern Mozambique.
	B Mid-Triassic to mid-Jurassic	Volcanics. Extrusion of Stormberg, Karoo, Swaziland basalts. Intrusives in Rhodesia, South America.
	S 200-155 m.y. (8, 10, 20)	Polar wander curves.
	S Post mid-Jurassic-pre mid-Cretaceous (13)	
	S Pre late Cretaceous 140 m.y. (2, 12)	Magnetic banding between Africa and East Antarctica.
	S Pre Neocomian (15) (early Cretaceous)	Marine sediments.
	S Pre Valanginian (10) (early Cretaceous)	Marine sediments.
6. EAST ANTARCTICA-INDIA	S Mid-Jurassic-mid-Cretaceous (13, 14, 21)	Polar wander curves.
	S Pre-Cenomanian (10) (late Cretaceous)	Marine sediments between Antarctica and India.
	B Albian, 100-105 m.y. (early Cretaceous) (14, 21)	Volcanics. Extrusion of Rajmahal Traps.
7. AFRICA-MADAGASCAR (probably archipelagic Cretaceous to Recent)	S Mid-Jurassic-mid-Cretaceous (14)	Polar wander curves.
	B ?Permian (35)	Rifting.
	B Early Jurassic (32)	Volcanics.
	S Jurassic-late Cretaceous (31); pre early Cretaceous (45)	Volcanics, rifting, sediments (by Turoonian open marine conditions between Madagascar and Africa).
	B Cretaceous (11)	Rifting in East Africa.
	S Late Mesozoic (10)	Faunal.
	S Late Cretaceous (10)	Volcanics present in East Africa and Madagascar.
	S Late Eocene (34)	Marine sediments in Mozambique Channel.
8. INDIA-MADAGASCAR	S Post mid-Cretaceous (14)	Polar wander curves for India and Madagascar.
	S 70-75 m.y. (41)	Magnetic anomalies; oldest anomaly, 30.
	S Campanian (10) (late Cretaceous)	Marine sediments between India and Madagascar.
	B Late Cretaceous-early Tertiary, 59-65 m.y. (10, 14, 21, 40)	Volcanics. Deccan Traps of western India.
	S Post late Cretaceous (10)	Marine faunas (see over).

<i>Continental Pair</i>		<i>Time of Break-up/Dispersal</i>	<i>Evidence</i>
9. INDIA/MADAGASCAR- AFRICA	S	Mid-Jurassic- mid-Cretaceous (10)	Polar wander curves.
	S	70-75 m.y. (41)	Magnetic anomalies; oldest anomaly, 30.
	S	Pre latest Cretaceous, 67 m.y. (15)	Magnetic banding in NW sector of Indian Ocean.
	S	40 m.y. (26)	Magnetic banding.
	S	Post late Cretaceous (10)	Faunas (marine invertebrates) of Coromandel Coast of India quite similar to those of Assam and South Africa in late Cretaceous but distinct from those from Narbada Valley in NW India. Faunas of NW India most similar to those of North Africa and Europe. Evidence suggests non-marine barrier between northern and southern Africa, eastern and western India.
10. AUSTRALIA-INDIA	B	Late Jurassic-early Cretaceous, 100-105 m.y. (9, 12, 14, 15)	Volcanics. Rajmahal Traps (NE India), Banbury (Perth Basin) and Ashmore Reef (Aust.) basalts, Broom Beds (tuffs, Canning Basin, Aust.).
	S	Early Cretaceous (9, 12, 15)	Marine sediments. First occurrence of marine sediments (during Mesozoic) in Perth Basin. Thick sequence of non-marine sediments as young as Jurassic in subsurface, southern Perth Basin.
	S	Pre early Tertiary (3)	Sediments on either side of Ninetyeast Ridge in Indian Ocean 'show a unified history and little or no relative motion since early Tertiary'.
	S	Pre mid to upper Oligocene (33, 36)	Submarine erosion occurring in Tasman sea evidenced by thinness or absence of Oligocene sediments in this area and the scoured oceanic surface below such sediments; mid to upper Oligocene sediments, when, present often intensely current-bedded, suggesting presence of submarine current.
	B	Latest Carboniferous- earliest Cretaceous (43)	Rifting in Western Australia.
	B	Permian-Neocomian (42)	Vulcanism, Banbury Basalt, latest Neocomian tholeiite.
	S	Late Jurassic (in NW part of Australia) to late Neocomian-Aptian (in SW Australia) (43)	Magnetic banding in Indian Ocean and initiation of marine transgression in Western Australia.
	S	Pre latest Jurassic (Tithonian) (44)	Sediments (oldest) overlying oceanic crust near Western Australian coast.
11. AUSTRALIA- NEW ZEALAND (probably archipelagic Cretaceous to Recent)	S	80 m.y. (4)	Magnetic banding between Campbell Plateau and W. Antarctica, Australia, and E. Antarctica indicates New Zealand moving north while Australia still attached to E. Antarctica.
	B	Paleocene-Eocene	Volcanics. Beginning of significant volcanic activity in eastern Australia that continue through much of the Tertiary.
	?	51 m.y. (3)	

The following papers are referred to in Table 1 under their respective numbers:

1. Jones, 1971
2. LePichon and Heirtzler, 1968
3. Wellman, McElhinny, and McDougall, 1969
4. Griffiths and Varne, 1972
5. Pitman, Herron and Heirtzler, 1968
6. Weissel and Hayes, 1971
7. Creer, 1970
8. Dietz and Holden, 1970
9. Veevers, 1971
10. Smith and Hallam, 1970
11. Sowerbutts, 1972
12. Tarling, 1971
13. Francheteau and Sclater, 1969
14. McElhinny, 1970
15. Veevers, Jones, and Talent, 1971
16. McElhinny and Wellman, 1969
17. Vilas and Valencio, 1970
18. Burke, Dessauvage, and Whiteman, 1971
19. Christoffel and Ross, 1970
20. Dietz and Sproll, 1970
21. McDougall and McElhinny, 1970
22. Dalziel and Elliot, 1971
23. Griffiths, 1971
24. Hamilton, 1964
25. Maxwell, *et al.*, 1970
26. Heirtzler, *et al.*, 1968
27. Reyment, 1969
28. Funnell and Smith, 1968
29. Dickson, Pitman, and Heirtzler, 1968
30. McGowran, 1971 (ms)
31. von der Borch, 1972
32. Flores, 1970
33. Kennett, *et al.*, 1972
34. Simpson, *et al.*, 1972
35. Kent, 1972
36. Carter and Landis, 1972
37. Creer, Embleton, and Valencio, 1969
38. Larson and LaFountain, 1970
39. Leyden, Bryan, and Ewing, 1972
40. Wellman and McElhinny, 1970
41. McKenzie and Sclater, 1971
42. Harrington, *et al.*, 1973
43. Veevers and Evans, 1973
44. Heirtzler, *et al.*, 1973
45. Green, 1972
46. Valencio and Vilas, 1972
47. Jones, 1972
48. Dingle, 1973

occurrence of magnetic anomalies in the intervening ocean basins, (3) the first differences in the polar wander paths of segments previously part of one continental plate, and (4) differences in the tectonostratigraphic provinces of two previously geologically similar and contiguous continental plates (see Smith and Hallam, 1970; and particularly Tarling and Tarling, 1971 for more detail on the dating methods mentioned above). Such data evidencing break-up and dispersal of the Gondwana continents since the Triassic are summarized in Table 1 and Figure 1 for each continental pair, except East Antarctica-West Antarctica (see discussion below). Figure 1 specifically indicates the variety of the data used to estimate the time of break-up of each continental pair, while Table 1 details that data, indicating whether break-up or active dispersal was underway.

Fragmentation within Gondwanaland began as early as the Triassic, but actual severance in terrestrial continuity between those parts of the southern continents connected in the late Palaeozoic (approx. 225 m.y. B.P.) was a late Mesozoic and even early Tertiary phenomenon (approx. 70-130 m.y. B.P.; see figures 1-2, 7-10, and Table 1). The first complete separation was apparently between Africa and East Antarctica in the late Jurassic or early Cretaceous (Heirtzler, *et al.*, 1968, Francheteau and Sclater, 1969; Dietz and Sproll, 1970; Smith and Hallam, 1970; Dietz and Holden, 1970; Dingle and Klinger, 1971; Heirtzler and Burroughs, 1971; Tarling, 1971; Sowerbutts, 1972; Jones, 1972; Dingle, 1973). Although not so well understood, the severance of any close alliance between India and Australia probably occurred in the early Cretaceous (Heirtzler, *et al.*, 1968; Veevers, 1971; Tarling, 1971; Veevers, Jones, and Talent, 1971; Crawford, 1971²), certainly not later than late Mesozoic (von der Borch, *et al.*, 1972). Thus the shortest dispersal route between Australia and the remaining continents during the late Mesozoic and much of the Paleogene was across Antarc-

² Crawford argues that during the Phanerozoic India was closely apposed to Africa with a seaway separating India and Australia. Just how broad such a water gap would have been is uncertain at present.

separation of continental masses (S in Table 1) with concomitant loss of non-marine dispersal pathways. Widespread occurrence of vulcanism and extensional faulting, sometimes accompanied by evaporite deposits, can be the first indication of continental break-up. Similarly, active separation between continental blocks is evidenced by: (1) the first widespread occurrence of marine sediments after a long period of continental sedimentation, (2) the first

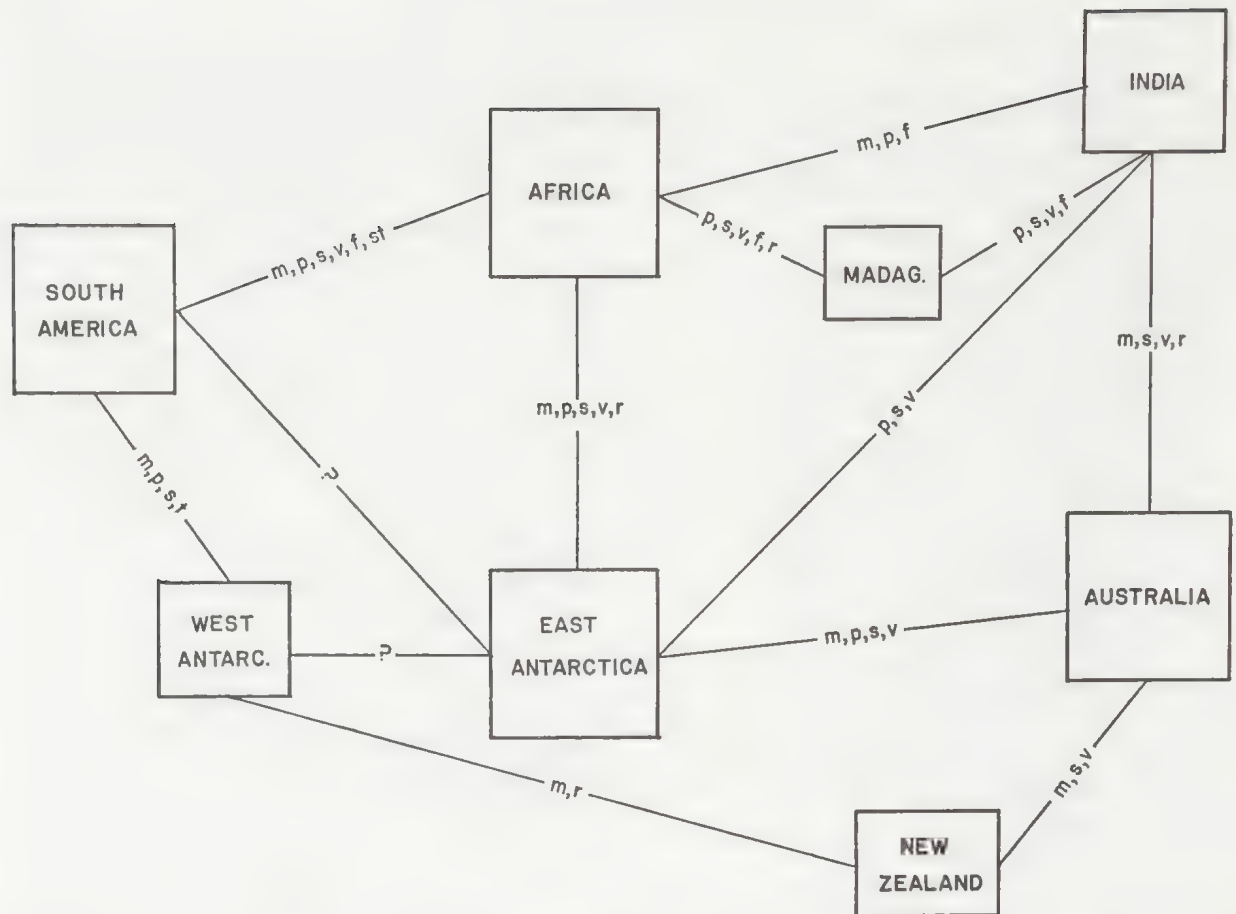


Fig. 1—Evidence available for timing the post-Paleozoic break-up and dispersal of Gondwanaland. The following symbols were used: m, magnetic anomalies on the seafloor; p, polar wander curves; s, widespread occurrence of marine sediments after long period of non-marine sedimentation and other sedimentological data; v, occurrence of widespread volcanism; f, faunal (both marine and terrestrial) similarities and differences; r, onset of major extensional rifting; t, similarity of tectonostratigraphic provinces; st, occurrence of widespread salt deposits.

tica. Asia, at this time, was as much as 30-50° north of Australia (Dietz and Holden, 1970; Tedford, 1973a; Jardine and McKenzie, 1972; Raven and Axelrod, 1972).

In the late Mesozoic (see figure 4), East Antarctica and Australia seemingly formed a continuous land mass (Jones, 1971; Le Pichon and Heirtzler, 1968; Smith and Hallam, 1970; McElhinny, 1970; Heirtzler, et al., 1968; Veevers, 1971; McGowran, 1971). Connection

at this time to South America, as to New Zealand, appears to have been archipelagic. Similarly a West Antarctic archipelago may have lain between South America and New Zealand (Fleming, 1962; Tedford, 1973a; Elliot, 1972). Yet unresolved and critical to late Mesozoic and Cenozoic reconstructions, however, is the precise relationship of West Antarctica to South America and East Antarctica. Many workers suggest that during much of the Mesozoic West Antarctica and New Zealand were all part of one plate's compressive margin (Elliot, in press, 1972), and must have developed in close proximity to a continental sediment source, East Antarctica and Australia (van der Linden, 1969), with the southern Andean Cordillera and the Antarctic Peninsula, although not necessarily a linear chain (Dalziel and Elliot, 1971, 1973), forming a link between these two continents. Severe disruption of this perhaps already archipelagic

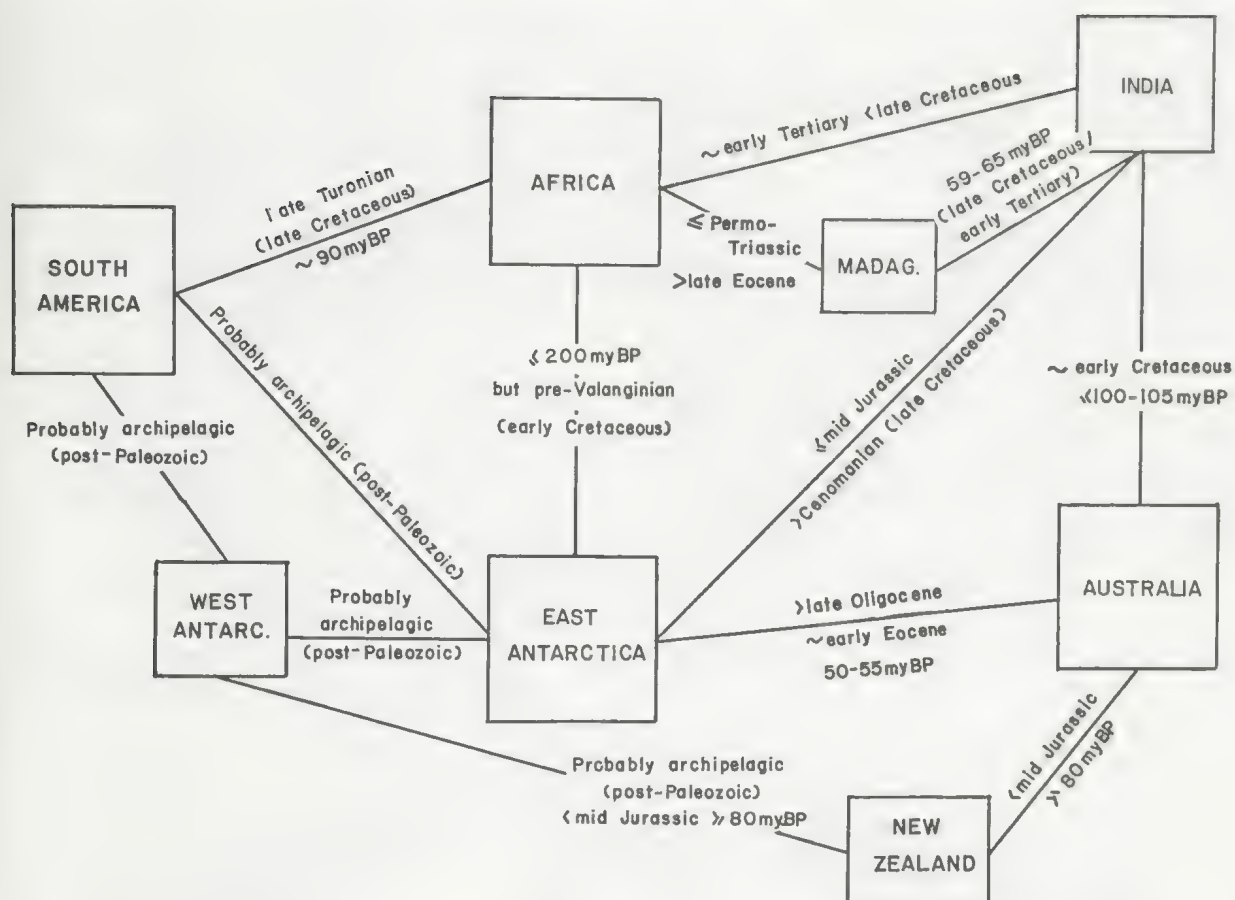


Fig. 2—Estimate of time of most recent severance of land connections between presently distinct continental masses, once part of Gondwanaland.

cordillera may have begun prior to 82 m.y. B.P. (Dalziel and Elliot, 1971, 1973) with transform or transcurrent faulting rotating the Ellsworth Mountains (now situated between East Antarctica and the Antarctic Peninsula) (Dalziel and Elliot, 1971, 1973; Elliot, 1972; Schopf, 1969). During the late Mesozoic and early Cenozoic, South America and West Antarctica may have approached one another more closely than at present (Dalziel and Elliot, 1973). Some workers, however, suggest that East and West Antarctica were independent entities during the Mesozoic, becoming closely apposed only in the Cenozoic (Beck, 1972). Others further suggest that the post-Jurassic tectonic histories of southern South America and West Antarctica have been decidedly independent

and that deformation of the Scotia Arc occurred prior to the late Mesozoic (Katz, 1973). Elliot (pers. comm., 1974) has pointed out that this does not necessarily mean that insular linkage was lacking between the two areas during the Mesozoic and part of the Cenozoic, however. More general agreement attends the positioning of New Zealand decidedly closer to Marie Byrd Land in West Antarctica until about 80 million years ago, when it apparently began its northward drift with the foundering of the Campbell Plateau and opening of the Tasman Sea (Griffiths, 1971; Griffiths and Varne, 1972). The opinion of most geologists dealing with these areas, however, despite the differing details of their reconstructions, is that any dispersal route involving West Antarctica from mid-Mesozoic to the Recent would probably have been archipelagic (Elliot, 1972; Jardine and McKenzie, 1972; Dalziel, pers. comm., 1973).

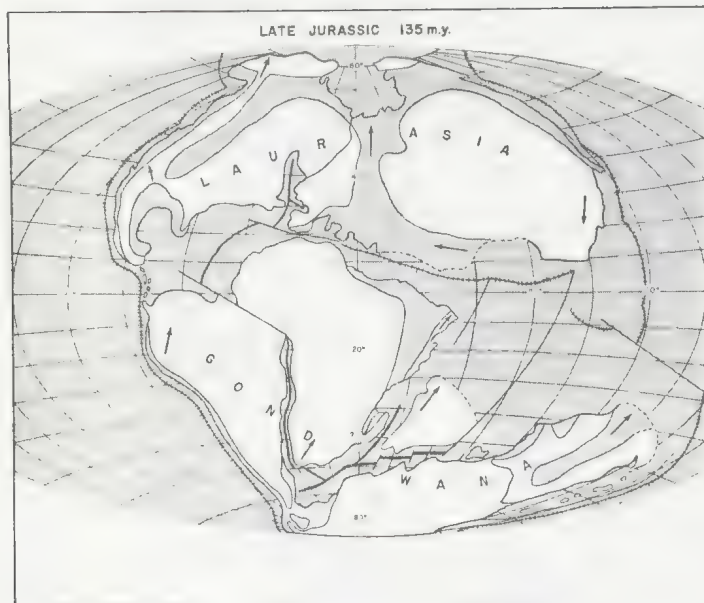
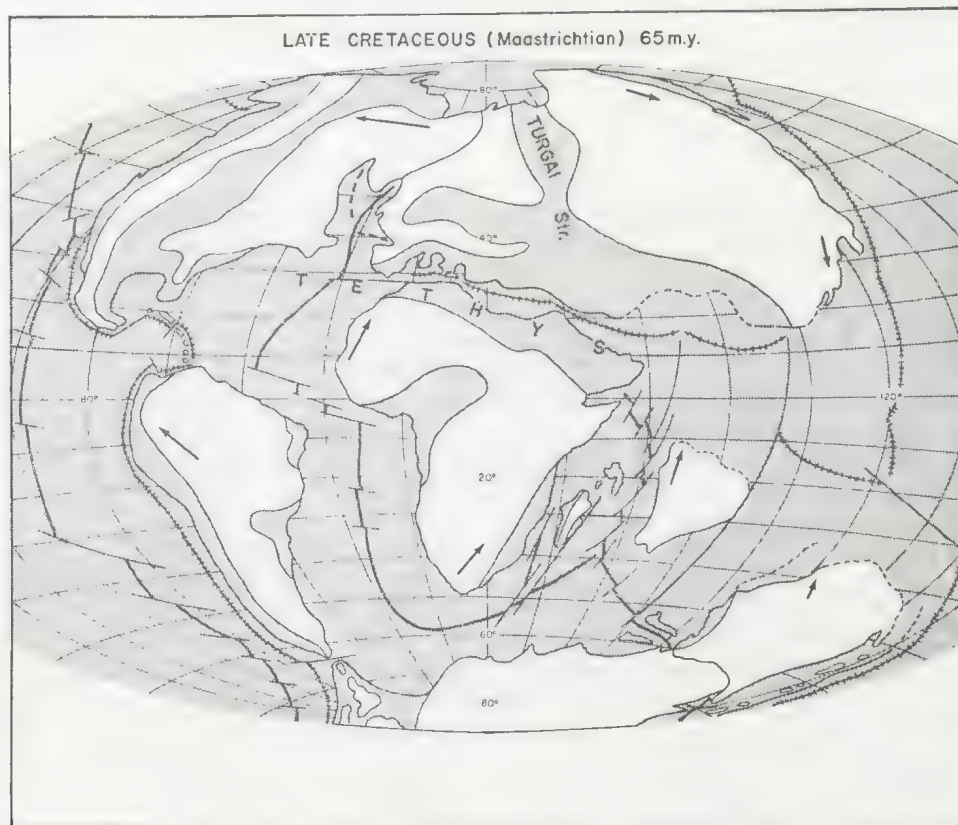


Fig. 3—Continental arrangement during the late Jurassic (135 m.y.) as modified from Tedford, 1973a. In such reconstructions, the earth's surface is divided into a series of crustal plates that move relative to each other. Three types of boundaries separate these plates: (1) transform faults (light lines) where the plates slide laterally past one another; (2) ridges (dark lines), where new molten rock is added to the edges of two plates and they subsequently move away from one another; and (3) trenches (hatched lines), where one plate slides beneath another. Arrows indicate direction of relative motion.

Fig. 4—Continental arrangement during the late Cretaceous (65 m.y.) as modified from Tedford, 1973a.



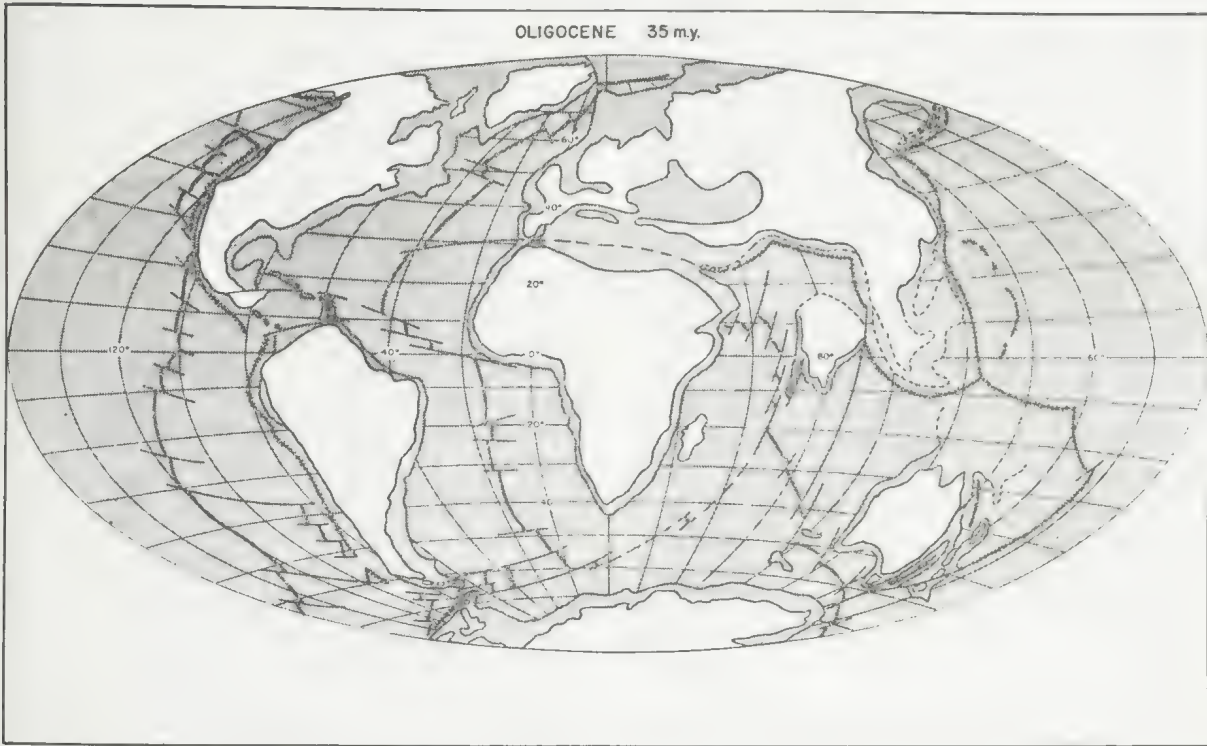
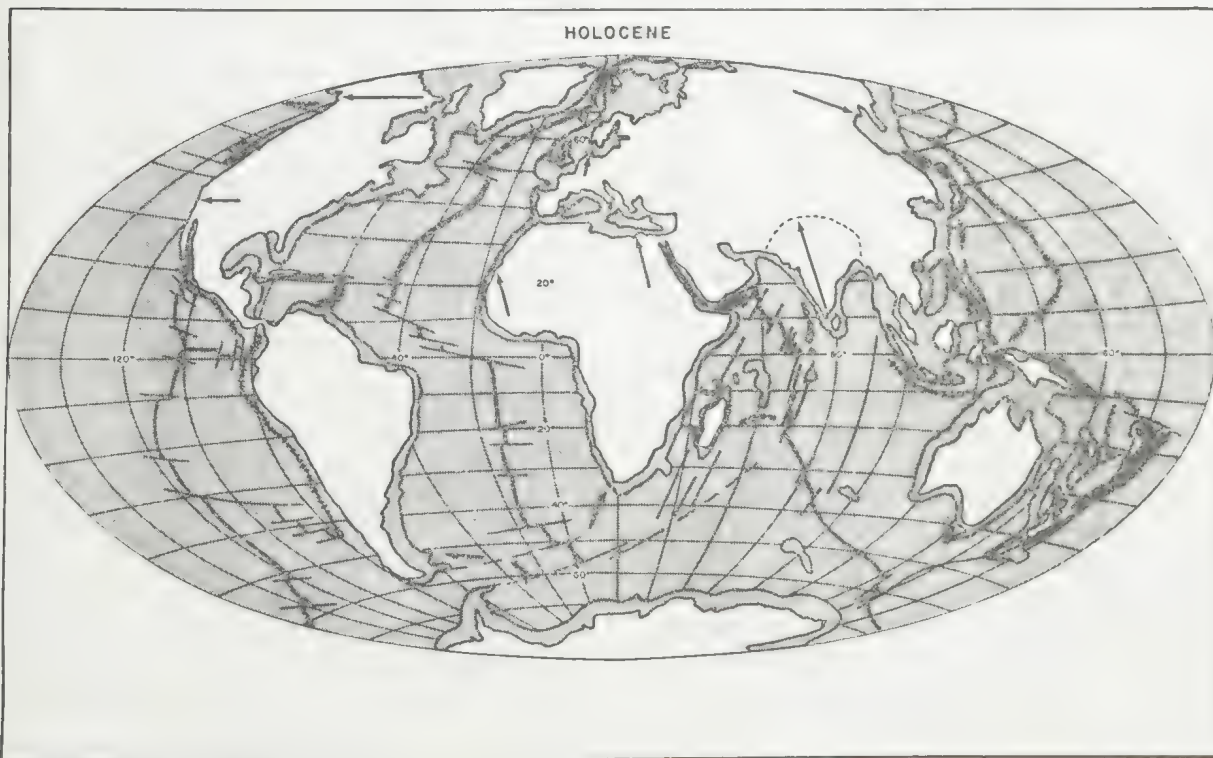


Fig. 5—Continental arrangement during the Oligocene (35 m.y.) as modified from Tedford, 1973a.

Fig. 6—Continental arrangement at present.



Only in the Tertiary, the early to mid-Eocene (50-55 m.y. B.P.), and certainly by the late Oligocene (Kennett, *et al.*, 1972), did Australia sever its connection with East Antarctica (Le Pichon and Heirtzler, 1968; Jones, 1971; Veevers, 1971; Smith and Hallam, 1970; Davies and Smith, 1971; McGowran, 1971; Vogt and Conolly, 1971; Griffiths and Varne, 1972; Weissel and Hayes, 1972) and begin its northward journey, which is still in progress (see figure 9). From a position of 60-70° south latitude (measured from Canberra) in the Cretaceous, Australia moved to within 10° of its present position (see figure 10) by the Miocene (Wellman, McElhinny, and McDougall, 1969; Veevers, Jones, and Talent, 1971; Raven and Axelrod, 1972). New Zealand continued separating from both Australia and West Antarctica, increasing the isolation that presently characterizes it. Thus, during the late Mesozoic and early Tertiary, the separation of Australia and New Zealand from their present Asian and most Indonesian neighbours was great with close apposition occurring only after the Oligocene (see Hamilton, 1972a-b; Haile and McElhinny, 1972; Stauffer and Gobbett, 1972; *contra* Ridd, 1971, and Audley-Charles *et al.*, 1972).

Indonesian Dispersal Route (Operative, Late Cenozoic)

The mid-Cenozoic close approach of Australia to Asia (including Southeast Asia, see Haile and McElhinny, 1972 and closely apposed Indonesia, see Ben-Avraham and Uyeda, 1973; Hamilton, 1972a-b), presented new possibilities for dispersal to and from Palaeo-archica. With Antarctica's movement south of the Australo-Antarctic Ridge and concomitant deterioration in its climate accompanying positioning closer to the pole, it was further isolated from Australia. Thus, its importance as a dispersal route declined as that of Indonesia increased. By the Miocene, the principal dispersal route for terrestrial organisms to and from Australia was the Indomalaysian Archipelago (McKenna, 1973), including the Philippines, much of which was subaerial by this time (Hamilton, 1972a; van Bemmelen, 1949; Grabau, 1926).

Throughout the Cenozoic the area between Southeast Asia and Australia has probably been dotted with islands, many of which have been ephemeral, occasionally disappearing down oceanic trenches or submerging along with older parts of ocean basins. In some senses a dispersal route of sorts probably existed across this archipelago in the Paleogene, but distances between islands as well as the total length of the route were much greater than at present and prohibitive in all but the rarest cases of non-marine vertebrate dispersal. Most of central and southern New Guinea, the leading edge of the Australian plate in the Paleogene, was underwater until the late Oligocene-early Miocene (Raven and Axelrod, 1972; Davies and Smith, 1971; Tedford, 1973a; Audley-Charles *et al.*, 1972). During the Miocene, a southward migrating island arc system collided with the northern edge of the Australian crustal plate (see figure 7 for explanation), adding the final, northern segment to form modern New Guinea (Hamilton, 1972b) and causing considerable uplift. By late Cenozoic, therefore, extensive emergent lowland areas and developing highlands were present in New Guinea. In the Indomalaysian area (extremely complex geologically) much of the Malay Peninsula, and at least parts of Sumatra, Java, Borneo, and Sulawesi were emergent during the early Cenozoic (Grabau, 1926; van Bemmelen, 1949; Kummel, 1961). Major parts of the Andaman-Sumatra-Java-Timor-Outer Banda-Seram chain of islands, however, are composed of uplifted subduction melanges (a jumble of sediments, volcanics, and metamorphics typifying an area where one major plate of the earth's crust is underthrusting another) produced during the Miocene and uplifted sometime later (Hamilton, 1972a-b; Katili, 1971). During the late Pliocene, folding further uplifted many of the previously homogeneous lowland areas in both Indonesia and New Guinea (Kummel, 1961), providing a mountainous, temperate dispersal route (Raven and Axelrod, 1972) between Asia and Australia, probably for the first time in the Mesozoic-Cenozoic. Further emergence during the Pleistocene concurrent with development of ice sheets elsewhere in the world, shortened water gaps, and made the Indo-

malayan area a very probable route for dispersal of terrestrial organisms.

Paleoclimatological Evidence

Antarctic Dispersal Route

Based on paleobotanical data, the climatic regime of the Antarctic Peninsula and East Antarctica was much less severe during the late Mesozoic and early Tertiary than at present. During the Jurassic, scouring rushes (Equisetales), ferns (Filicales), cycadophytes (Cycadophyta), and conifers are known from several localities in Grahamland, West Antarctica (Plumstead, 1962, 1964; Bibby, 1966). Unfortunately, only one post-Triassic, pre-Tertiary flora is known from East Antarctica (Victoria Land); it contains a cycadophyte as well as three types of conifers very similar to those known from India, East Africa, and Australia in strata of early Jurassic age. Such assemblages in both East and West Antarctica suggest equable, moist conditions, warmer than at present, particularly in order to accommodate the cycadophytes, which were experiencing latitudinal restriction in the Northern Hemisphere during the Jurassic (Plumstead, 1964). The presence of freshwater actinopterygian fish in lower Jurassic sediments of East Antarctica (Schaeffer, 1972) lends corroborative evidence for more equable, certainly non-glacial Mesozoic conditions in parts of Antarctica. Mega and microfloral evidence indicates that at least two families of ferns (Cyatheaceae and Schizaeaceae), several conifers (*Araucaria*, *Agathis*, *Podocarpus*) (Andrews, 1961) and angiosperms including the Southern Beech (*Nothofagus*), mustards (Cruciferae), Myrtaceae, Proteaceae, Loranthaceae, and possibly *Drimys* (Winteraceae) were growing on Seymour Island in West Antarctica during the Cretaceous (Cranwell, 1959). Likewise, floras very tentatively dated as early to mid-Tertiary from King George and Seymour Islands, also in West Antarctica, contain scouring rushes, ferns, conifers (including *Araucaria*), as well as a variety of angiosperms, including *Nothofagus* (Adie, 1953; Cranwell, 1959; Plumstead, 1964). Approximately ninety per cent of the

dicotyledons in these floras have non-entire margins and small leaves, more typically reminiscent of temperate plant species living in mild to cool conditions at present (Axelrod and Bailey, 1968). Again, the flora of East Antarctica is not as well known, with only two lower Tertiary localities: one in the McMurdo Sound area (Cranwell et al., 1960; McIntyre and Wilson, 1966) and a second near Prydz Bay (Kemp, 1972a-b) on the Australian side of East Antarctica. Much of the pollen from these localities is similar to that from West Antarctica. The McMurdo sample derived from Eocene erratic boulders and recycled sediments in the Ross Sea includes conifer, palm, *Podocarpus*, and *Nothofagus* pollen, among others. Probable *in situ* late Oligocene sediments in the Ross Sea have recently produced many of the same elements with *Nothofagus* and Podocarpaceae dominant and minor percentages of Proteaceae and Myrtaceae. Noticeably absent is pollen of groups presently found on subantarctic islands such as Gramineae, Cyperaceae, Umbelliferae, or Compositae (E. Kemp, pers. comm., 1974). The Prydz Bay pollen flora derived from Cretaceous-Eocene sediments is decidedly more varied, containing at least 21 genera including *Nothofagus* (*fusca*, *menziesii*, and *brassi*), *Podocarpidites*, *Gleicheniidites*, *Osmundacites*, and *Cyanthidites* (Filicales) reminiscent of dominant taxa in the early Tertiary Australian flora. Certainly as diverse a flora as this seems incompatible with a continent-wide glaciation prior to the Oligocene.

In summary, fossil floras from East and West Antarctica, although admittedly rare, suggest a temperate climate for parts of this region capable of supporting sizeable trees and a diverse assemblage of plants during much of the Mesozoic, possibly as late as the Miocene and even the Quaternary on the Falkland Islands, which support no forests today (Axelrod, 1960). Much of this same flora that occurred in Antarctica was also present in southern South America, Kerguelen Island, New Zealand, and parts of Australia (Axelrod, 1960) during the early to mid-Tertiary. This flora was apparently rather similar to the temperate and cool temperate rainforests of present-day southern Chile, Patagonia, south-

eastern Australia, Tasmania, New Zealand, and New Caledonia.

Additional information of paleoclimatic significance has been derived from geologic and fossil invertebrate data. Recent electron micrograph studies of sand grain surface features based on submarine core samples from the Subantarctic Pacific, has been interpreted to indicate that glaciation, although probably of limited extent, was underway in parts of Antarctica as early as the Eocene (Geitzenauer *et al.*, 1968; Gram, 1969; Margolis and Kennett, 1970, 1971a-b; Kennett and Brunner, 1973). Apparently glacially transported sand grains were rafted away from the Antarctic as part of icebergs and deposited as the ice melted. Accompanying the first occurrence of such sands, Mandra (1969, 1971; also in Mandra and Mandra, 1970) noticed a drop in silicoflagellate species diversity, which was interpreted as indicative of cooling of the southern oceans at that time. In the early and middle Oligocene cores, ice rafted sand is no longer a dominant feature, if present at all, and silicoflagellate diversity in such sediments is higher than in immediately older sediments, indicating warmer seas than in the earlier Tertiary, perhaps owing to the establishment of the circum-Antarctic current at about this time.

Additional geologic evidence mustered to suggest an Eocene glaciation in West Antarctica has been recovered from Marie Byrd Land. LeMasurier (1970) has noted the occurrence of hyaloclastites, volcanic rocks known to form at present only in subglacial or subaqueous eruptions of lava. Accumulations of hyaloclastites up to 400 metres thick with no evidence of subaerial lava flows have been interpreted to indicate ice at least that thick in some places during the Eocene, providing, of course, that such volcanics belong to a single flow and providing that Le Masurier is correct in assuming that this area in West Antarctica was above sea level when such lavas were extruded. Other hyaloclastite accumulations in the same area indicate glaciation from the Oligocene to the Pleistocene where ice thickness may have reached 1200 metres by the Pliocene. Lava flows dated as late Miocene in the Jones Mountains of West Antarctica are known to overlie

"consolidated glacial deposits and extensive areas of glacially scoured bedrock" (Newell, 1972, p. 64). Even though much of West Antarctica (particularly the Antarctic Peninsula) supported *Nothofagus* dominated forests perhaps as late as the Miocene, glaciation may have been underway in limited areas as early as the Eocene. The evidence for widespread early Tertiary glaciation, however, based on such sedimentological and volcanic data has recently been challenged by Mercer (1973), who believes the botanical evidence for both segments of Antarctica suggest nothing more than local glaciation until 3·4-6 m.y. B.P. Certainly by 4-5 m.y. B.P. glaciation on a continental scale is suggested by widespread erosion surfaces over much of the Ross Sea continental shelf, evidently produced by a grounded ice shelf (Hayes, *et al.*, 1973), but glacial history of Antarctica prior to this time has yet to be resolved.

Unfortunately, owing to the lack of post-Jurassic paleomagnetic data from East Antarctica (primarily because of the lack of post-Jurassic rocks cropping out above the present ice cover, as well as the paucity of samples even from West Antarctica) there is as yet no coherent picture of the South Pole position with respect to Antarctica during the late Mesozoic and early Tertiary. A number of papers (Francheteau and Sclater, 1969; McElhinny and Wellman, 1969; Crawford, 1971; McElhinny, 1970; among others) summarizing available paleomagnetic evidence derived from continents exclusive of Antarctica, including Australia, present no consensus on East Antarctica's mid to late Mesozoic or Early Tertiary latitudinal position. Data reported by McElhinny and Wellman (1969) and Francheteau and Sclater (1969) do not exclude the possibility of a high latitude (yet *outside* the Antarctic Circle) dispersal route along the Victoria Land and Wilkes Land coast of East Antarctica during the early Tertiary. Almost all reconstructions, however, place West Antarctica within the Antarctic Circle during late Mesozoic and Cenozoic, and yet the evidence of *Nothofagus*-dominated forests in this area is incontrovertible. Either such forests were able to withstand a yearly cycle with three months of

perpetual darkness or parts of East and West Antarctica lay at a lower latitude. This only points out the need for additional geophysical data before the latitudinal position of both major segments of Antarctica during the Mesozoic and Cenozoic is clear.

Indomalaysian Dispersal Route

In marked contrast to the cool, temperate floras of Paleogene Antarctica, are floras from the late Mesozoic and Cenozoic Indomalaysian area. Although no thorough, current summary of the Southeast Asian and Indonesian fossil floras is available, a number of early papers (Barbour, 1929; Colani, 1917, 1920; Edwards, 1923; Göppert, 1854; Holden, 1916; Kräusel, 1922, 1925, 1926; Seward, 1941; Andrews, 1961 among others) discussing leaf, wood, and fruit evidence and more recently papers (Chaney, *et al.*, 1963; Endo, 1964; Endo and Fujiyama, 1966; Germeraad, *et al.*, 1968; Jones *et al.*, 1966; Kon'no, 1966; Manten, 1969) describing the pollen, allow an estimation of the late Mesozoic and Cenozoic vegetation of this area. By the Cretaceous, several elements now characteristic of the warm, humid tropical lowlands of Southeast Asia and Indonesia were present there. Germeraad, *et al.* (1968) reported *Nypa* palm, now restricted to the mangrove swamps of the Indomalaysian region, from late Cretaceous sediments of Sarawak. Paleogene floras of northern Viet Nam (Colani, 1920), Borneo (Kräusel, 1925), Sumatra (Kräusel, 1922), and Java (Göppert, 1854) contain many of the tropical elements found in floras of these areas today: Palmae, Pandanaceae, *Ficus*, *Quercus* (closely related to tropical oaks in this genus), Piperaceae, Anacardiaceae or Annonaceae, Moraceae, Musaceae, Dipterocarpaceae, *Rhizophora* (mangrove), among others. Some of these early floras contain only tropical forms, but others exhibit a mixture of these and more temperate elements such as *Taxus*, *Phoebe*, *Betula*, *Ben-zoin* (Colani, 1920), characteristic of the Himalayas or more northern areas in Asia, and probably represent elements of upland floras of Indonesia and Southeast Asia. Miocene and younger floras from the Indomalay region are more diverse, containing a large

number of presently tropical taxa, with first occurrences of such forms as Sapindaceae, Sterculiaceae, and definite Anacardiaceae among others. To the north of Southeast Asia, however, cool to warm temperate assemblages had differentiated by the early Cenozoic. Floras of northern Thailand (Endo and Fujiyama, 1966), Siberia, Manchuria, Korea, and Japan (Barbour, 1929; Chaney, *et al.*, 1963; Endo, 1964; Endo and Fujiyama, 1966) during early to mid-Cenozoic, commonly contained such forms as *Sequoia*, *Taxodium*, *Pinus*, *Alnus*, *Populus*, Betulaceae, Ulmaceae, Platanaceae, Juglandaceae, Ericaceae as well as some families (e.g. Fagaceae, Aceraceae) held in common with the more southerly areas.

Undoubtedly, a detailed re-evaluation of much of the early work on Indomalaysian paleofloras must be carried out before the floral history of this area will be understood. However, with recent palynological investigation confirming many of the earlier identifications of Cenozoic tropical forms based on leaves, wood, and fruit, apparently several families of plants presently restricted to the tropics occurred in Southeast Asia as early as the Cretaceous and Paleogene. During the entire history of the modern avian families, and certainly during the Neogene, then, much of the Indomalaysian area probably supported a warm, humid tropical flora, not so different (at the family level, at least) from that occupying the same area today.

Australia

Instrumental in the development of the Australian avifauna were the dramatic changes in the climatic regime affecting Australia during post-Palaeozoic times. Raven and Axelrod (1972), Gill (1961), Dorman (1966), and Burbidge (1960) summarize much of the geochemical, floral, faunal, pedologic, and lithologic data that are employed to reconstruct Australia's past climate.

Most important as temperature indicators are radioisotope, paleobotanical, and faunal data. Paleotemperature determinations, based on oxygen isotope studies (O^{18}/O^{16} ratios) of Cretaceous belemnites from Australia and New Zealand (Stevens and Clayton, 1971), indicate

decreasing near shore water temperatures from an early Cretaceous (ca. 110 m.y. B.P.) high to an Albian-Cenomanian (ca. 100 m.y. B.P.) low (N.Z. samples: from 42° S. present latitude, ca. 16° C., comparable to averages N.Z. temperatures at 39-40° S.; Australian samples from Lake Eyre region at 28° S. present latitude, ca. 15° C., comparable to temperatures at 41° S. at present). Temperatures rose again in the Coniacian-Santonian (ca. 18° C. from samples taken at 42° S. present latitude in N.Z., comparable to temperatures at 36-37° S. at present) but began dropping again during the Campanian (ca. 70-75 m.y. B.P.), continuing into the Paleocene. Oxygen isotope studies on shells of several different molluscan genera (collected from localities in southern Victoria between the present 38-39° S. latitudes) suggest a continued drop in temperatures into the late Eocene (to ca. 12-16° C.) followed by a rise to a Cenozoic maximum in the mid-Miocene (22-25° C.), probably accompanying the onset of Australia's northward drift from Antarctica. Since the Miocene, temperatures have continued to drop, with minor fluctuations, to the present (12° C. for southern Victoria) (Dorman, 1966; Dorman and Gill, 1959a-b).

Cretaceous and early Tertiary floras indicate widespread temperate conditions evidenced by mixed forests of austral gymnosperms and evergreen angiosperms (Podocarpaceae, Araucariaceae, Araliaceae, Myrsinaceae, Protaceae, Winteraceae, Atherospermataceae, Epacridaceae, Malvaceae, Loranthaceae, Sapindaceae, Casuarinaceae, Myrtaceae, and *Nothofagus* (Fagaceae); Raven and Axelrod, 1972). During this time *Araucaria*, now restricted in Australasia to areas in New Guinea and coastal eastern Australia, where average temperature of the coldest month is 11° C., grew in Tasmania and southern Victoria. *Nothofagus brassi*, presently restricted to altitudes above 3000 feet in New Guinea, was widespread in the early Tertiary of southern and eastern Australia. Mid-Tertiary floras, on the other hand, indicate restriction of such temperate forests (*Nothofagus-Araucaria* dominated) to the southern and northern margins of the continent and the dominance of the *Eucalyptus-Acacia* assemblage

that contained such additional taxa as *Casuarina*, *Melaleuca*, *Hakea*, and *Eremophila*. Most of this mid to late Cenozoic flora appears to have been (and still is) adapted to the drier, more seasonal conditions that became prevalent on a continental scale as Australia moved into the high pressure "horse latitudes" with their accompanying xeric climates. Sclerophyll forest, savannas, and more arid vegetation covered much of Australia, while rain forests were present along the eastern, mountainous edge of the continent (Tedford, 1973a).

In New Guinea, with the emergence of extensive lowlands in the late Oligocene-early Miocene, a rich tropical flora with strong Malaysian affinities and quite distinct from that of mainland Australia gained a foothold. Only much later in the Pliocene and Pleistocene, accompanying the tectonism that produced extensive temperate, montane environments as well as xeric conditions in areas of rain shadow (Raven and Axelrod, 1972), was there much exchange between New Guinea and Australia. At this time, too, northern temperate forms (e.g. *Castanopsis*, *Rhododendron*) were able to enter New Guinea and Australia from Asia for the first time along the temperate uplands created by the mid to late Cenozoic tectonism.

Invertebrate faunas (particularly foraminifera, mollusca, and echinoids) indicate, by faunal composition and diversity, a Tertiary temperature maximum in the early Miocene.³ Only at this time were any of the larger foraminifera (*Trybliolipidina*, *Cycloclypeus*) present in the southern Australian Bass Strait Province. Likewise, the first major reef building episode in Australia since the Palaeozoic began in the Miocene when Old World reef communities, as well as other tropical invertebrates

³ The mid-Tertiary temperature rise in Australia, indicated by invertebrate faunas and oxygen isotope ratios, correlates well with the drift of this continent northward into lower, more tropical latitudes. Throughout most of the world, temperatures steadily (with minor fluctuations) declined throughout the Cenozoic. Once Australia neared its present position sometime in the Miocene and its northward drift slowed, its climate deteriorated in synchrony with the rest of the world, climaxing in the low temperatures of the Pleistocene.

(Palmiere, 1971), colonized the Australian continental shelf (Newell, 1971, 1972). In Victoria, many groups of marine molluscs (cones, cowries and volutes in particular) exhibited increased diversity in the early to mid-Miocene, as well as a marked increase in Indopacific taxa (Darragh, 1973; Darragh, 1974). By the late Miocene (Cheltenhamian), however, temperatures began dropping as indicated by the striking reduction both in number of individuals and in diversity of both molluscs and echinoderms. By Kalimnan times (about 6 m.y. B.P.), the marine invertebrate faunas in the continental shelf areas around Australia were essentially modern (Brown, Campbell, and Crook, 1968), indicating temperatures not so different from those today.

Vertebrate faunas, too, indicate changes in humidity and temperature in much of Australia during the Cenozoic. Lungfish, confined to a small area of southeastern Queensland in the late 19th century (Grigg, 1964), are present in Cretaceous sediments in southern Victoria (Schaeffer, 1969) and at a number of localities of Tertiary age in the Australian interior. Teleost fish are known from most of the localities producing lungfish, yet many of these areas no longer support permanent streams. Crocodilians, now rarely found further south than Rockhampton on the northeast coast and the Ord River (Gill, 1961) in the northwest, ranged into northern South Australia and Victoria in the Tertiary, demonstrating greater humidity and yearly minimum temperatures than encountered today in those areas. Diverse fossil avifaunas from the mid to late Tertiary of interior South Australia and the Northern Territory (see figures 3-4, table II, and later section of paper) include flamingos (Phoenicopteridae) and even aningas (Miller, 1963b, 1966a), the latter restricted to warm regions with permanent streams and abundant stream-side vegetation today and probably for some time in the past (Rich, 1972, 1974). Fossil mammals, similarly, suggest a more humid environment during the Tertiary (see Tedford, 1973a for discussion of the fossil marsupial faunas of Australia). In interior South Australia and the Northern Territory a diverse assemblage of medium to large-sized mammals are known

from probable mid-Miocene sediments and include koalas, several taxa of diprotodontids (extinct marsupial family closely related to the kangaroos), wombats, phalangers, thylacoleonids, monotremes, and even porpoises among others (see Stirton, Tedford, and Woodburne, 1968; Tedford, 1973a-b). A number of smaller forms including dasyurids, phalangerids, and peramelids were also present. The occurrence of koalas, as well as the diversity of mammals in these mid-Tertiary faunas, suggests a more heavily vegetated, more humid environment during the mid-Tertiary than presently exists in these areas today, a suggestion certainly corroborated by other vertebrate as well as floral evidence.

Summary

During the Mesozoic and as late as mid-Eocene (ca. 50 m.y. B.P.), geological and paleobotanical data suggest that a southern dispersal route across East Antarctica and archipelagic West Antarctica was the most likely connection between Australia and other continents. Southeast Asia during this period was probably far to the north, perhaps as much as 30-50° of latitude. At least many of the islands making up West Antarctica, as well as parts of East Antarctica, supported substantial forests dominated by several kinds of gymnosperms, including *Araucaria* and *Podocarpus* as well as a number of angiosperms including *Nothofagus*. Part of this route, possibly along the Victoria Land and Wilkes Land coast of East Antarctica and appropriate islands in West Antarctica, may have lain north of the Antarctic circle, thus providing a route having some daylight hours throughout the entire year. By the end of the Miocene, Australia had severed its connections with East Antarctica and drifted north to within 10° of its present position, strengthening the dominance of the Indomalayan dispersal route, which has been most influential during the latter part of the Cenozoic. Simultaneous with northward drift, climatic changes affecting the Australian continent brought about a shift from the early Cenozoic cool temperate flora dominated by proteads and *Nothofagus* to the mid to late Cenozoic (including the present) zoned vegetation com-

posed of arid (in interior Australia), tropical (in New Guinea and Northern Australia), and cool temperate (in southeastern Australia and Tasmania) elements. Such marked changes in Australia's geographic position, its climate and floras, and its links with the rest of the world, undoubtedly have had a tremendous effect on its Cenozoic vertebrate faunas, including its birds.

Origin of the Non-passeriform Avifauna of Australia

Australian Avifaunal Composition

The living terrestrial and fresh-water non-passeriform avifauna of Australia and New Guinea is composed of some 44 families, of which the only endemics are the emu and cassowary (Casuariidae: *Dromaius* and *Casuarius*) and the collared hemipode (Pedionomidae) (see Table 3). If those birds restricted to the Australia-New Guinea-Southwest Pacific (excluding New Zealand) area are considered, then the megapodes (Megapodiidae) and owl frogmouths (Aegothelidae) can be added to the list of endemic families. In addition, a few distinct subfamilies are endemic to Australia and/or New Guinea and the Southwest Pacific, including the Cercopsinae, Loriinae, Cacatuinae, and Micropsittinae, all except the first, members of the Psittacidae (parrots). At the generic level, 34 taxa (exclusive of those in the above-mentioned families and subfamilies) are endemic to Australia and/or New Guinea alone (see Table 2) and an additional 28 are endemic to Australia and/or New Guinea and the Southwest Pacific (again excluding New Zealand). The fossil record adds two families not present in Australia today: the Dromornithidae, composed of large to truly gigantic ratite birds endemic to Australia, and the Phoenicopteridae (flamingos), both of which survived into the Pleistocene in Australia; flamingos, of course, yet survive in several parts of the world.

History of the Australian Non-Marine Avifauna (Figures 7-8)

Early Cretaceous (perhaps late Jurassic; J. Warren, pers. comm., 1974) lacustrine sedi-

ments in southeastern Victoria have produced feathers (Talent, *et al.*, 1966; Waldman, 1970) and record an early presence of birds on the Australian continent. These, together with a few Eocene-Oligocene penguin bones from southeastern Australia (Simpson, 1946, 1957, 1959, 1965, 1970; Gill, 1959a-b; Finlayson, 1938; Anonymous, 1959), a single record of an unidentified bird bone (now lost) from early Tertiary sediments near Sunnybank, southeastern Queensland (Hill and Denmead, 1960, p. 349; Houston, 1967, p. 85), and a feather impression as well as a possible forelimb of a bird from near Wannon, western Victoria (Chapman, 1910; David, 1950), constitute the early record of birds in Australia. By mid-Miocene, however, a moderately diverse assemblage of modern avian families was present, known from several localities (see Table 3) in the interior of Australia and includes:⁴

- Dromornithidae (mihirung birds) (Rich, 1973)
- Dromaiinae (emus) (Rich, 1973)
- Pelecanidae (pelicans) (Miller, 1966b)
- Phalacrocoracidae (cormorants) (Rich, 1973)
- Accipitridae (an eagle) (Rich, 1973)
- Anatidae (ducks) (Rich, 1973)
- Phoenicopteridae (flamingos) (Miller, 1966a)
- cf. Gruidae (cranes) (Stirton, *et al.*, 1968)
- cf. Rallidae (rails) (Stirton, *et al.*, 1968)
- Charadriiformes, undetermined family (shorebirds) (Rich, 1973)
- Laridae (gulls) (Stirton, *et al.*, 1968)
- Burhinidae (thick knees, stone curlews) (Stirton, *et al.*, 1968; Rich, 1973)
- Caprimulgiformes (nightjars, frogmouths) (Rich, 1973).

The avifauna, even at this time, was strikingly modern with only the dromornithids (4-5 genera in the Miocene) and the flamingos (2 genera in the Miocene) forming an odd

⁴ To complete the list of Australian Miocene fossil birds, Wilkinson, H. E., 1969, reported an albatross (Diomedidae) from Victoria. Since this is a marine bird, however, it will not be considered in the above discussion.

TABLE 2

Endemics to Australia-New Guinea-Southwest Pacific (after Peters 1931-1945)

- † Australia and/or New Guinea
 # Australia and/or New Guinea and Southwest Pacific
 * Australia and/or New Guinea, Southwest Pacific, Asia

FAMILY LEVEL

- † Casuariidae (including †*Casuarius* and †*Dromaius*)
 † Pedionomidae (†*Pedionomus*)
 # Megapodidae (#*Megapodius*, †*Leipoa*, †*Alectura*, #*Telegalla*, #*Aepyodius*)
 * Podargidae (**Podargus*)
 # Aegothelidae (#*Aegothales*)
 * Hemiprocnidae (**Hemiprocne*)

SUBFAMILY LEVEL

- † Ceropsinae (†*Cereopsis*)
 # Loriinae (#*Trichoglossus*, #*Pseuteles*, †*Glossopsitta*, #*Opopsitta*, †*Lathamus*, #*Chalcopsitta*, †*Pseudeos*, #*Domicella*, #*Charmosyna*, †*Oreopsittacus*, †*Neopsittacus*, #*Psittaculirostris*)
 # Cacatuinae (#*Probosciger*, †*Calyptorhynchus*, †*Callocephalon*, #*Cacatua*, †*Eolophus*, †*Nymphicus*)
 # Microsittinae (#*Microsittia*)

GENERIC LEVEL

- # *Zonerodius* (Ardeidae)
 * *Xenorhynchus* (Ciconiidae)
 † *Anseranas* (Anatidae, Plectropterinae)
 † *Stictonetta* (Anatidae, Anatinae)
 † *Malacorhynchus* (Anatidae, Anatinae)
 # *Salvadorina* (Anatidae, Nyrociniae)
 # *Chenonetta* (Anatidae, Anserinae)
 † *Biziura* (Anatidae, Oxyurinae)
 # *Henicopernis* (Accipitridae, Elaninae)
 † *Lophoictinia* (Accipitridae, Milvinae)
 † *Haemirostra* (Accipitridae, Milvinae)
 * *Haliastur* (Accipitridae, Milvinae)
 † *Erethrorhynchus* (Accipitridae, Accipitrinae)
 † *Harpyopsis* (Accipitridae, Buteoninae)
 # *Synoicus* (Phasianidae)
 † *Anurophasis* (Phasianidae)
 # *Eulabeornis* (Rallidae)
 * *Rallina* (Rallidae)
 # *Tribonyx* (Rallidae)
 * *Amaurornis* (Rallidae)
 * *Poliolimnas* (Rallidae)
 † *Rallcula* (Rallidae)
 # *Gymnocrex* (Rallidae)
 † *Megacrex* (Rallidae)
 † *Peltohyas* (Charadriidae)
 † *Cladorhynchus* (Recurvirostridae)
 * *Esacus* (Burhinidae)
 # *Stiltia* (Glareolidae)
 # *Procelsterna* (Laridae)
 # *Gygis* (Laridae)
 * *Ptilinopus* (Columbidae, Treroninae)
 # *Megaloprepia* (Columbidae, Treroninae)
 * *Ducula* (Columbidae, Treroninae)
 † *Lopholaimus* (Columbidae, Treroninae)
 † *Petrophassa* (Columbidae, Columbinae)

- * *Macropygia* (Columbidae, Columbinae)
 * *Chalcophaps* (Columbidae, Columbinae)
 † *Phaps* (Columbidae, Columbinae)
 † *Ocyphaps* (Columbidae, Columbinae)
 † *Lophophaps* (Columbidae, Columbinae)
 † *Geophaps* (Columbidae, Columbinae)
 † *Histriophaps* (Columbidae, Columbinae)
 † *Leucosarcia* (Columbidae, Columbinae)
 † *Geopelia* (Columbidae, Columbinae)
 # *Gymnophaps* (Columbidae, Columbinae)
 # *Reinwardtoena* (Columbidae, Columbinae)
 # *Gallicolumba* (Columbidae, Columbinae)
 # *Henicophaps* (Columbidae, Columbinae)
 † *Trugon* (Columbidae, Columbinae)
 # *Otidiphaps* (Columbidae, Columbinae)
 # *Caloenas* (Columbidae, Columbinae)
 # *Goiira* (Columbidae, Gouirinae)
 # *Eclectus* (Psittacidae, Psittacinae)
 # *Geoffroyus* (Psittacidae, Psittacinae)
 † *Polytelis* (Psittacidae, Psittacinae)
 # *Aprosmictus* (Psittacidae, Psittacinae)
 # *Alisterus* (Psittacidae, Psittacinae)
 † *Platycercus* (Psittacidae, Psittacinae)
 † *Purpureicephalus* (Psittacidae, Psittacinae)
 † *Psephotus* (Psittacidae, Psittacinae)
 † *Neophema* (Psittacidae, Psittacinae)
 † *Melopsittacus* (Psittacidae, Psittacinae)
 † *Pezoporus* (Psittacidae, Psittacinae)
 † *Geopsittacus* (Psittacidae, Psittacinae)
 † *Psittarchas* (Psittacidae, Psittacinae)
 † *Psittacella* (Psittacidae, Psittacinae)
 * *Loriculus* (Psittacidae, Psittacinae)
 # *Scythrops* (Cuculidae, Cuculinae)
 * *Ninox* (Strigidae)
 # *Uroglauis* (Strigidae)
 * *Eurostopodus* (Caprimulgidae)
 # *Dacelo* (Alcedinidae, Daceloninae)
 # *Tanyptera* (Alcedinidae, Daceloninae)
 # *Melidora* (Alcedinidae, Daceloninae)
 † *Clytoceyx* (Alcedinidae, Daceloninae)

element leaving no living representatives in Australia. Both of the latter groups survived into the Pleistocene but not the Recent.

By the Pliocene cassowaries (*Casuarius*) had differentiated and were present in New Guinea (Plane, 1967) while a third genus of flamingo, *Phoeniconaias*, occurred for the first and only time in Australia (*Phoeniconotius* is not known from sediments younger than Miocene, while *Phoenicopterus* persisted into the Pleistocene).

Pleistocene faunas add the first known Australian occurrences of the Podicepsidae (*Podiceps*, grebes), the Threskiornithidae (spoonbills), cf. *Cygnus atratus* (Black Swan), the Megapodiidae (mound builders, including a gigantic form nearly twice the size of any living megapode, from several localities in eastern Australia), the Phasianidae (quail), the Falconidae (falcons), the Turnicidae



Fig. 7—Tertiary and Mesozoic localities producing fossil birds in Papua-New Guinea and Australia: Awe (1); Bullock Creek (2); Riversleigh (3); Alcoota (4); Peak Downs (5); Chinchilla (6); Lake Kanunka (7); Lake Palankarinna (8, 9); Eurinilla Creek and Lake Pinpa (10); Port Noarlunga (11); Christie's Beach (12); Pritchard Brothers' Quarry (13); Mt. Gambier (14); Devil's Den (15); Spring Creek (Minhamite) (16); Beaumaris (17); Endurance Pit (18); Lake Ngapakaldi (19); Lake Pitikanta (20); Redbank Plains (21); Kangaroo Well (22); Bugaldi (near Coonabarabran) (23); Redruth, Wannon (24); and Koonwarra (25).

(*Turnix*, bustard quail), the Pedionomidae (plains wanderers), the Scolopacidae (sandpipers), the Chionidae (*Chionis*, sheathbill), the Columbidae (pigeons, doves), the Psittacidae (parrots and allies), the Tytonidae

(*Tyto*, barn owl), and several passeriforms. A number of additional groups reported by DeVis (1888a-b, 1889a-b, 1891a-c, 1905; in Gregory, 1906) and Longman (1945) need restudy to ascertain their taxonomic positions (Phalacrocoracidae, **Ciconiidae**, Anatidae, Rallidae, **Otididae**⁵).

Thus, at least 23 of the 44 families constituting the modern non-passeriform avifauna of Australia have mid to late Cenozoic histories there, while two additional families have Miocene to Pleistocene records but no modern representatives in the Australian avifauna. Most certainly the lack of a Tertiary record for many other families is owing to the small

⁵ Taxa named in boldfaced type indicate earliest known occurrence in Australia.



Fig. 8—Quaternary localities producing fossil birds in Papua-New Guinea and Australia: Diamantina River (no specific locality known) (1); Cassidy Locality (2); Warburton River Localities (3); Cooper's Creek Localities (4); Lake Callabonna (5); Thorbindah (6); Cud-die Springs (7); Ashford Caves (Bone Cave) (8); Bingara (9); Canadian Lead (Gulgong) (10); Walli and Wellington Caves (11); Wombeyan Caves (Guineacore) (12); Lake Menindee (13); Lake Tandou (14); Baldina Creek (15); Normanville (Salt Creek) (16); Kangaroo Island (17); Henschke's Cave and Victoria Cave (18); Penola (19); Mt. Gambier (20); King Island (21); Madura Cave (22); Scott River (23); Mammoth Cave (24); Darling Downs (Kings Creek, Warwick) (25); Drover's Cave (26); Gore (27); Buchan Caves (28); Weeke's Cave (29); Brother's Island, Pt. Lincoln (30); and Lancefield (31).

number of Cenozoic vertebrate producing localities presently known in Australia.

Owing to the limited nature of the fossil record in Australia, first occurrences of avian families and genera have no special significance regarding which dispersal route was being used, or in what direction movement occurred. By the Miocene, when the first extensive avifaunas are known in Australia, Southeast Asia and Australia were close enough to one another for avifaunal interchange to have been underway. Unfortunately we know almost nothing of the earlier Australian terrestrial avifaunas, which could have marked significance regarding South American affinities, enhanced by the existence of an Antarctic dispersal in the early Tertiary.

TABLE 3

Summary of the Avifaunas from Australian Cenozoic Localities¹
(if reference not cited, from Rich, 1973)

TERTIARY
EOCENE

- Queensland Interbedded sediments in unnamed basalt overlying Darra Fm. and underlying Sunnybank Fm. at Sunnybank, Aves, undetermined (now lost). Cribb, *et al.*, 1960.
- South Australia *Christie's Beach*. 'Transitional Marl' Member, base of Blanche Point Marls, *Palaeudyptes cf. antarcticus* (Spheniscidae, penguin). Simpson, 1946, 1957.
- South Australia *Port Noarlunga Jetty*. Banded Marl Member of Blanche Point Marls, *Palaeudyptes cf. antarcticus*. Simpson, 1946, 1957.

OLIGOCENE

- South Australia *Mount Gambier*. Gambier Limestone. Spheniscidae (penguin). Simpson, 1946, 1957.
- South Australia *Pritchard Brothers' Quarry*. Gambier Limestone, 7½ miles WNW of Mt. Gambier, *Palaeudyptinae* (penguin). Simpson, 1946, 1957.

MIOCENE

- South Australia *Snake Dam Locality*. Mooloorina Station, cf. Dromornithidae (mihirung bird, egg shell). M. Woodburne, M. Archer, pers comm., 1973.
- South Australia *Lake Pinpa*. Unnamed unit; *Phalacrocorax* sp. (Phalacrocoracidae, cormorant), Anatidae (duck), Burhinidae (thick-knee, stone curlew).
- South Australia *Eurinilla Creek*. Unnamed unit; Anatidae (duck), cf. Phoenicopteridae (flamingo).
- South Australia *Lake Palankarinna*. Etadunna Formation, Ngapakaldi fauna (including localities LFM Loc. 9, U.C.M.P. Locs. V-5762, V-5763, V-5764, V-5765, V-5770, V-5771, Mammalon Hill); *Pelecanus tirarensis* (Pelecanidae, pelican), Phalacrocoracidae or Anhingidae (cormorant or darter), Phoenicopteridae, gen. et sp. undet. (flamingo), *Phoeniconotus eyrensis* (Phoenicopteridae), (undet.), *Oxyura* (Anatidae, duck), cf. Gruidae (crane), Rallidae (rail), Burhinidae (thick-knee), Charadriiformes (shorebirds), Laridae (gull), Stirton, Tedford, and Woodburne, 1967.
- South Australia *Lake Pitikanta*. Etadunna Formation, Ngapakaldi fauna (including Discovery Basin U.C.M.P. V-5774 and U.C.M.P. V-6150); *Phoenicopterus novaehollandiae* (Phoenicopteridae, flamingo). Miller, 1963b.
- Queensland *Riversleigh*. Carl Creek Limestone, Riversleigh fauna; Dromornithidae (new gen., new sp.) (mihirung bird).
- Victoria *Devil's Den* (Glenelg River). Glenelg Group, Balcomian Stage, north of Dartmoor; *Anthropodyptes gilli* (Spheniscidae, penguin). Simpson, 1959.
- South Australia *Kangaroo Well*. Unnamed formation, Kangaroo Well fauna, Aves, undetermined. Stirton, Tedford, and Woodburne, 1967.
- South Australia *Lake Ngapakaldi, Leaf Locality*. Wipijiri Formation, Kutjamarpu fauna (U.C.M.P. V-6213); *Dromaius* (Casuariidae, emu), Dromornithidae (mihirung bird); *Ngapakaldi 2* (U.C.M.P. V-6213), Dromornithidae. Stirton, Tedford, and Woodburne, 1967.
- Northern Territory *Bullock Creek*. Camfield Beds, Bullock Creek fauna; Dromornithidae (1 new gen., 2 new sp.) (mihirung birds).

¹ Those taxa prefaced by (x) were last studied by DeVis, and further study is needed to ascertain their correct taxonomic position.

- Northern Territory *Alcoota*. Waite Formation, Alcoota fauna (including Paine Quarry U.C.M.P. V-6345, Rochow Locality U.C.M.P. V-6349); cf. *Dromaius* (Casuariidae, emu), Dromornithidae (3 new gen., 3 new sp.) (mihirung bird), Accipitridae (eagle).
- New South Wales *Bugaldi*, diatomaceous earth deposit. cf. Aegothelidae (owlet-frog-mouth).
- Victoria *Beaumaris*. Sandringham Sands, Cheltenhamian Stage, Beaumaris fauna; Spheniscidae (penguin), ?*Pseudaptenodytes macraei* (Spheniscidae, penguin), ?*P. minor*, *Diomedea thyridata* (Diomedidae, albatross). Simpson, 1965, 1970; Wilkinson, 1969.
- Victoria *Spring Creek, Minhamite*. ?Cheltenhamian Stage; *Pseudaptenodytes macraei* (Spheniscidae, penguinidae).
- PLIOCENE
- South Australia *Lake Palankarinna, Lawson-Daily Quarry (Lawson Quarry)*, Mampurdu Sands, Palankarinna fauna (U.C.M.P. V-5769); *dromaius ocyus* (Casuariidae, emu), Dromornithidae (mihirung bird). Miller, 1963a.
- New Guinea *Awe*. Otibanda Formation, Awe fauna; *Casuarius* sp. (Casuariidae, cassowar). Plane, 1967.
- South Australia *Lake Kanunka*. Katipiri Sands, Kanunka fauna (U.C.M.P. V-5772, V-5773, V-5855); *Dromaius* (Casuariidae, emu), *Pelecanus* (Pelecanidae, pelican), *Phalacrocorax* (Phalacrocoracidae, cormorant), (2 sp.), *Anhinga novaehollandiae* (Anhingidae, anhinga, snake bird), *Phoeniconaias gracilis* (Phoenicopteridae, flamingo), *Phoenicopus ruber* (Phoenicopteridae) Anatidae (duck), cf. *Aythya* (Anatidae, duck). Stirton, Tedford, and Woodburne, 1967.
- Queensland *Peak Downs*. *Dromornis australis* (Dromornithidae, mihirung birds). Owen, 1874, 1879b.
- Queensland *Chinchilla*. Chinchilla Sands, Chinchilla fauna; *Dromaius* (Casuariidae, emu), *Pelecanus conspicillatus* (= *P. proavus*) (Pelecanidae, pelican), *Haliaeetus melanoleucos* (Phalacrocoracidae, cormorant), (x) *Xenorhynchus nanus* (Ciconiidae, stork), (x) *Anas elapsa* (= *Nettion elapsus*, Brodkorb)¹ (Anatidae, duck), (x) *Biziura exhumata* (Anatidae, duck), (x) *Dendrocygna* (Anatidae, duck), (x) *Nyroca reclusa* (= *reperta*, = *Aythya reclusa*, Brodkorb) (Anatidae, duck), (x) *Nyroca robusta* (= *Aythya robusta*, Brodkorb) (Anatidae, duck), *Gallinula* (= *Tribonyx mortierii reperta* (Rallidae, rail) (Olson, 1974), *Fulica atra* (Rallidae, rail) (Olson, 1974), DeVis, 1888-1905.
- PALEOGENE(?)
- Victoria *Redruth* (Wannon River). Ironstone, 'wing of a struthious bird', Aves, undetermined (David, 1950), feather impression (Chapman, 1910).
- MIDDLE TERTIARY
- Tasmania *Endurance Pit*. cf. Dromornithidae (mihirung birds), footprints. (Rich and Green, 1974).
- QUEENSLAND
- Darling Downs
- Dromaius* cf. *novaehollandiae* (Casuariidae, emu)
 Anhingidae (darter, J. van Tets, pers. comm., 1973)
 (x) *Palaeopelargus nobilis* (Ciconiidae, stork)
 (x) *Platalea subternis* (Threskiornithidae, spoonbill)
 (x) *Dendrocygna validipennis* (Anatidae, duck)
 (x) *Nyroca* sp. (Anatidae, duck)
 (x) *Necrastur alacer* (Accipitridae, hawk, eagle)
 (x) *Taphaeus brachialis* (= *Uroaetus* = *Aquila*) (Accipitridae, eagle)
Progura gallinacea (Megapodiidae, mound builder) (van Tets, 1974a)
Gallinula mortierii reperta (Rallidae, rail) (Olson, 1974) — ?
 Warwick
 (x) *Lithophaps ulnaris* (Columbidae, pigeon) DeVis, 1888-1905.

1. Generic reallocation most recently provided by Brodkorb, 1963, 1964, 1967, 1971a.

Gore

Progura naracoortensis (Megapodiidae, mound builder). Longman, 1945; van Tets, 1974a.

King's Creek, Darling Downs

(x) *Dromaius patricus* (? = *D. novaehollandiae*) (Casuariidae, emu)

(x) *Taphaetus brachialis* (= *Uroaetus* = *Aquila*) (Accipitridae, hawk, eagle). DeVis, 1888-1905.

Diamantina (general locality; could be any of several places along the Diamantina River)
Genyornis (Dromornithidae, mihirung bird).

Thorbindah, Paroo River

Dromaius (Casuariidae, emu)

Genyornis, cf. *newtoni* (Dromornithidae, mihirung bird).

NEW SOUTH WALES

Ashford Caves (Bone Cave) (U.C.M.P. V-67237, U.C.M.P. V-5545)
Aves, undetermined.

Bingara

Dromaius (Casuariidae, emu). L. Marcus, pers. comm., 1973.

Canadian Lead

Dromornithidae (mihirung bird). Etheridge, 1889; Owen, 1879b.

Cuddie Springs

Genyornis cf. *Newtoni* (Dromornithidae, mihirung bird). Anderson and Fletcher, 1934.

Lake Menindee (including Rifle Range Loc. U.C.M.P. V-67233, U.C.M.P. V-5371, V-67185, V-67186, V-67187)

Dromaius (Casuariidae, emu).

Lake Tandou

Dromaius (Casuariidae, emu)

Podiceps (Podicepedidae, grebe)

cf. *Ciconiiformes* (herons, storks, ibises)

cf. *Cygnus atratus* (Anatidae, swan)

cf. *Columbidae* (pigeon).

Wellington Caves (including Bone Cave, Mitchell's Cave, Phosphate Mine (in part U.C.M.P. V-5538))

(x) *Dromaius patricus* (? *D. novaehollandiae*) (Casuariidae, emu)

Casuarius lydekkeri (Casuariidae, cassowary)

Dromornithidae (mihirung bird)

Progura gallinacea (Megapodiidae, mound builder). Mitchell, 1839; Miller, 1962; Rich, 1973; van Tets, 1974a.

Walli Caves

Progura gallinacea (Megapodiidae, mound builder). van Tets, 1974a.

Wombeyan Cave (Guineacor) (in part U.C.M.P. V-5537)

Aves, undetermined

Dromaius (Casuariidae, emu)

Progura gallinacea (Megapodiidae, mound builder). van Tets, 1974a.

VICTORIA

Buchan Cave (J. van Tets, pers. comm., 1973)

Rallidae (rails)

Coturnix sp. (Phasianidae, quail)

Alcedinidae (kingfishers)

Passeriformes (song birds, perching birds).

Lancefield

Dromornithidae (mihirung bird).

TASMANIA

King Island

Dromaius minor (Casuariidae, emu). Spencer and Kershaw, 1910.

SOUTH AUSTRALIA

Baldina Creek (near Burra)

Dromornithidae (mihirung birds).

Brother's Island, Pt. Lincoln

Dromornithidae (mihirung bird).

Cooper's Creek (includes several localities collected primarily by J. W. Gregory and later parties from the University of California, Berkeley) (Katipiri Sands, Malkuni Fauna).

University of California Localities (Miller, 1963-1966; Rich, 1973)

- | | |
|------------------|--|
| U.C.M.P. Site 2 | (U.C.M.P. V-5379) Unkumilka Waterhole
<i>Dromaius</i> sp. (Casuariidae, emu)
<i>Phalacrocorax</i> sp. (Phalacrocoracidae, cormorant). |
| U.C.M.P. Site 3 | (U.C.M.P. V-5378) Between White Crossing and Site 2
<i>Dromaius</i> sp. (Casuariidae, emu)
<i>Phalacrocorax</i> sp. (Phalacrocoracidae, cormorant; middle-sized sp., lg. sp.). |
| U.C.M.P. Site 4 | (U.C.M.P. V-5380)
<i>Anhinga novaehollandiae</i> (Anhingidae, darter/snake bird)
<i>Phalacrocorax</i> sp. (Phalacrocoracidae, cormorant; middle-sized sp., lg. sp.)
Anatidae (duck). |
| U.C.M.P. Site 5 | (U.C.M.P. V-5381) Pirranna Soakage
<i>Dromornithidae</i> (mihirung birds)
<i>Phalacrocorax</i> (Phalacrocoracidae, cormorant; middle-sized sp.)
Anatidae (small sp.) (duck). |
| U.C.M.P. Site 7 | (U.C.M.P. V-5859)
<i>Phalacrocorax</i> sp. (Phalacrocoracidae, cormorant; middle-sized sp.)
<i>Pelecanus conspicillatus</i> (Pelecanidae, pelican)
Anatidae (duck)
<i>Grus</i> sp. (crane). |
| U.C.M.P. Site 8 | (U.C.M.P. V-5860)
<i>Dromaius</i> sp. (Casuariidae, emu)
<i>Dromornithidae</i> (mihirung birds)
<i>Phalacrocorax</i> sp. (lg. sp.)
<i>Pelecanus conspicillatus</i> (Pelecanidae, pelican)
Anatidae (swan) |
| U.C.M.P. Site 9 | (U.C.M.P. V-5861) Katipiri Waterhole (= Kuttipirra)
<i>Dromaius</i> sp. (Casuariidae, emu)
<i>Dromornithidae</i> (mihirung birds)
<i>Phalacrocorax</i> sp. (Phalacrocoracidae, cormorant, middle-sized sp.)
Anatidae (swan). |
| U.C.M.P. Site 10 | (U.C.M.P. V-5869)
<i>Anhinga novaehollandiae</i> (Anhingidae, darter/snake bird)
<i>Phalacrocorax</i> sp. (Phalacrocoracidae, cormorant)
<i>Platalea</i> sp. (Threskiornithidae, spoonbill). |
| U.C.M.P. Site 14 | (U.C.M.P. V-5866)
<i>Anhinga novaehollandiae</i> (Anhingidae, darter)
<i>Phalacrocorax</i> sp. (Phalacrocoracidae, cormorant)
<i>Phoenicopiterus ruber</i> (Phoenicopteridae, flamingo). |
| U.C.M.P. Site 16 | (U.C.M.P. V-5868)
<i>Phalacrocorax</i> sp. (Phalacrocoracidae, cormorant)
<i>Pelecanus conspicillatus</i> (Pelecanidae, pelican)
Anatidae (swan). |

U.C.M.P. Site 18 (U.C.M.P. V-6147)
Dromaius sp. (Casuariidae, emu)
Phalacrocorax sp. (Phalacrocoracidae, cormorant)
Pelecanus conspicillatus (Pelecanidae, pelican)
 Anatidae (duck).

Malkuni Waterhole (U.C.M.P. V-5382)
Pelecanus conspicillatus (Pelecanidae, pelican).

Markoni Locality (U.C.M.P. V-5382)
 Dromornithidae (mihirung birds)
Podiceps sp. (Podicepedidae, grebes)
Phalacrocorax sp. (Phalacrocoracidae lg. sp.)
Tyto (Tytonidae, barn owl).

J. W. Gregory Localities (DeVis 1888-1905; in Gregory, 1906)

East of Pirani

(x) *Biziura exhumata* (Anatidae, duck).

Emu Camp (= Malkuni waterhole)

cf. *Genyornis newtoni* (Dromornithidae, mihirung bird).
 (x) *Phalacrocorax gregorii* (Phalacrocoracidae, cormorant)
 (x) *P. vetustus*
 (x) *Archaeocynus lacustris* (= *Cygnus lacustris*, Brodkorb) (Anatidae, swan)
 (x) *Biziura exhumata* (Anatidae, duck)
 (x) *Chenopsis nanus* (= *Cygnus lacustris*, Brodkorb) (Anatidae, swan).

Lower Cooper

Anhinga novaehollandiae (Anhingidae, darter)
 (x) *Phalacrocorax gregorii* (Phalacrocoracidae, cormorant)
 (x) *P. vetustus*
 cf. *Dromaius novaehollandiae* (Casuariidae, emu)
 (x) *Xenorhynchopsis tibialis* (Ciconiidae, stork)
 (x) *Anas gracilipes* (= *Nettion gracilipes*, Brodkorb) (Anatidae, duck)
 (x) *Archaeocynus lacustris* (= *Cygnus lacustris*, Brodkorb) (Anatidae, swan)
 (x) *Chenopsis nanus* (= *Cygnus lacustris*, Brodkorb) (Anatidae, swan)
 (x) *Nettapus eyrensis* (Anatidae, duck).

Lower Cooper Locality 2

Dromaius sp. (Casuariidae, emu)
 Dromornithidae (mihirung birds).

Lower Cooper Locality 3

Dromaius sp. (Casuariidae, emu).

Lower Cooper Locality 4

(x) *Dromaius patricus* (cf. *D. novaehollandiae*) (Casuariidae, emu).

Lower Cooper Locality 5

(x) *Asturaetus furcillatus* (= *Plioaetus furcillatus* Richmond) (Falconidae, falcon).

Lower Cooper Locality 6

(x) *Baza gracilis* (= *Aviceda gracilis*, Brodkorb) (Falconidae, falcon).

Cooper Creek

Anhinga laticeps (Anhingidae, darter)
Pelecanus grandiceps (Pelecanidae, pelican).

Patteramordu (= Red Bluff Locality of U.C.M.P.)

(x) *Anas strenua* (= *Nettion strenum*, Brodkorb) (Anatidae, duck).

Unduwampa

- (x) *Xenorhynchopsis minor* (Ciconiidae, stork)
- (x) *Archaeocygnus lacustris* (= *Cygnus lacustris*, Brodkorb) (Anatidae, swan)
- (x) *Chenopsis nanus* (= *Cygnus lacustris*, Brodkorb) (Anatidae, swan).

Wankamaminna

- (x) *Phalacrocorax gregorii* (Phalacrocoracidae, cormorant)
- (x) *Archaeocygnus lacustris* (= *Cygnus lacustris*, Brodkorb) (Anatidae, swan).

Wurdulumankula (Wurdulmankula)

- (x) *Dromaius patricus* (? cf. *D. novaehollandiae*) (Casuariidae, emu)
- (x) *Phalacrocorax gregorii* (Phalacrocoracidae, cormorant)
- P. carbo* (J. van Tets, pers. comm., 1973)
- (x) *P. vetustus*
- (x) *Xenorhynchopsis minor* (Ciconiidae, stock)
- (x) *Xenorhynchus nanus* (Ciconiidae)
- (x) *Ibis conditus* (= *Carphibis condita*, Brodkorb) (Threskiornithidae, ibis)
- (x) *Archaeocygnus lacustris* (= *Cygnus lacustris*, Brodkorb) (Anatidae, swan)
- (x) *Chenopsis nanus* (= *Cygnus lacustris*, Brodkorb) (Anatidae, swan)
- (x) *Nyroca effodiata* (= *Aythya effodiata*, Brodkorb) (Anatidae, duck)
- (x) *Leucosarcia proevis* (Columbidae, pigeon).

Henschke's Quarry Cave, Naracoorte

- Progyura naracoortensis* (Megapodiidae, mound builder). van Tets, 1974a.

Kangaroo Island

- Dromaius novaehollandiae diemenianus* (Casuariidae, emu). (Condon, 1973).

Lake Callabonna (Lower level)

- Dromaius* sp. (Casuariidae, emu)
- Genyornis newtoni* (Dromornithidae, mihirung bird).

Lake Callabonna (Upper level)

- Phalacrocorax* sp. (Phalacrocoracidae, cormorants).

Lake Eyre (exact locality unknown)

- (x) *Ocyplanus proeses* (Laridae, gull). DeVis in Gregory, 1906.

Mount Gambier Range

- Dromornithidae (mihirung birds).

Normanville (= Salt Creek)

- Dromornithidae, cf. *Genyornis newtoni* (mihirung bird).

Penola

- Dromornithidae, cf. *Genyornis newtoni* (mihirung bird).

Victoria Cave, Naracoorte (van Tets and Smith, 1974)

- Dromaius* sp. (Casuariidae, emu)
- Progyura naracoortensis* (Megapodiidae, mound builder)
- Leipoa ocellata* (Megapodiidae, mound builder)
- Coturnix pectoralis* (Phasianidae, quail)
- C. australis*
- Coturnix* sp. (Phasianidae, quail)
- Turnix varia* (Turnicidae, button quail)
- Pedionomus torquatus* (Pedionamidae, plains wander)
- Rallus philippensis* (Rallidae, rail)
- Peltohyas australis* (Charadriidae, plovers)
- Tringa glareola* (Scolopacidae, sandpiper, stilt, curlew)
- Gallinago hardwickii* (Scolopacidae, sandpiper, stilt, curlew)

Calidris ruficollis (Scolopacidae, sandpiper, stilt, curlew)
Chionis minor (Chionidae, sheath-bill)
Pezoporus wallicus (Psittacidae, parrot)
Tyto novae-hollandiae (Tytonidae, barn owl)
Gymnorhina tibicen (Passeriformes, song birds).
Gymnorhina tibicen (Passeriformes, song birds)

Warburton River Localities (Katipiri Sands, Malkuni Fauna)

Cassidy Locality (U.C.M.P. V-5539)
 cf. *Genyornis* (Dromornithidae, mihirung bird).

Green Bluff Locality (U.C.M.P. V-5775)

Dromaius sp. (Casuariidae, emu)
Phalacrocorax (Phalacrocoracidae, cormorant; lg. sp.)
 Anserinae (goose)
 Accipitridae (hawk, eagle).

Kalamurina

Dromaius sp. (Casuariidae, emu)
 Dromornithidae, cf. *Genyornis* (mihirung bird)
 (x) *Phalacrocorax gregorii* (Phalacrocoracidae, cormorant)
 (x) *P. vetustus*
 (x) *Anas gracilipes* (= *Nettion gracilipes*, Brodkorb) (Anatidae, duck)
 (x) *Taphaeus lacertosus* (= *Icthyophaga lacertosus* (van Tets, 1974c)
 (Accipitridae, eagle)). DeVis, 1888-1905; Rich, 1973.

Lookout Locality (U.C.M.P. V-5776)

Phalacrocorax sp. (middle-sized sp., lg. sp.) (Phalacrocoracidae, cormorant).

Marcus Locality

Phalacrocorax sp. (Phalacrocoracidae, cormorant; middle-sized sp., lg. sp.)
 cf. *Pelecanus* sp. (Pelecanidae, pelican).

Pundrakadarinna Soakage (U.C.M.P. V-5777)

Phalacrocorax sp. (Phalacrocoracidae, cormorant).

Warburton River

(x) *Pelecanus validipes* (Pelecanidae, pelican). Etheridge, 1894.

Weeke's Cave (Nullarbor Plain)

Platibis flavipes (Threskiornithidae, spoonbill)
Accipiter fasciatus (Accipitridae, hawks)
Falco cenchroides (Falconidae, falcon)
Turnix sp. (Turnicidae, bustard quail)
Cinclorhamphus cruralis, *C. mathewsi*, *Poephila guttata*, *Artamus leucorhynchus* (Passeriformes, song birds). van Tets, 1974b.

WESTERN AUSTRALIA

Labrinth Cave

Aves, undetermined.

Madura Cave

Aves, undetermined.

Mammoth Cave

Dromornithidae (mihirung bird).

Scott River

?Dromornithidae (mihirung bird), egg. Butler, 1969; Rich, 1973.

Previous Opinions Regarding Origin of the Australian Avifauna

In studying the Australo-Papuan avifauna three decades ago, Mayr (1941, 1944a-b, 1945b) concluded that it had been derived from the north, primarily southeastern Asia, with colonization occurring throughout the Cenozoic (see figure 9a). He recognized several groups of invaders, which he believed to represent different colonizations, oldest to most recent. The oldest invasion (early to mid-Tertiary at the latest, Mayr, 1944a) was reflected by the most unique groups in the living non-passeriform avifauna of Australia, including the Casuariidae (containing *Casuarius* and *Dromaius*), Megapodiidae, Loriinae, Cacatuinae (= Kakatocinae), Platycercinae, and Podargidae. Mayr noted that the nearest relatives of these six groups were uncertain, but argued that none were any more closely related to South American families than to Old World families. His second and more recent wave of colonists included the Pedionomidae (collared hemipodes) along with several passeriform families. The third wave consisted of a number of genera endemic to Australo-Papua, which he believed were Miocene or Pliocene arrivals, and included: *Synoicus* (Phasianidae), *Geopelia* (Columbidae), *Irediparra* (included in *Jacana*, Jacanidae), *Notophox* (included in *Ardea*, Ardeidae), *Dupetor* (Ardeidae), *Erythroriorchis* (Accipitridae), *Uroaetus* (= *Aquila*, Accipitridae), *Lophoictinia* (Milvinae), *Syma* (included in *Halcyon*, Alcedinidae), *Dacelo* (Alcedinidae), *Tanysiptera* (Alcedinidae), *Cacomantis* (Cuculidae), *Misocalius* (included in *Chrysococcyx*, Cuculidae), *Chaleites* (included in *Chrysococcyx*, Cuculidae), and *Eudynamis* (Cuculidae). Fourth and fifth waves included taxa that are presently only specifically, or subspecifically distinct, or indistinguishable from southeast Asian forms (Pliocene to Recent arrivals, according to Mayr). Such ideas viewed against a backdrop of stable continents were reasonable and remained so into the late 1950's. With the development during the last fifteen years of the concepts of continental drift, sea-floor spreading, and plate tectonics, it has become apparent that two

major routes may have existed that non-marine vertebrates could have employed in reaching or leaving Australia during the late Mesozoic and Cenozoic: the Antarctic as well as the Indomalaysian. With this additional information provided by geology, one of Mayr's basic assumptions, that of continental stability, is undermined, and his ideas regarding the origin of the Australian avifauna require re-examination.

Such re-evaluation has been initiated in papers by Serventy (1972, 1973), Cracraft (1972, 1973), Schodde and Calaby (1972), and Mayr (1972) himself. Serventy suggested such forms as *Dromaius* (emus), possibly *Anseranas* (Magpie Goose), the Megapodiidae (mound builders), the Podargidae (frogmouths), as well as several parrot subfamilies (Loriinae, Cacatuinae, Platycercinae (included in the Psittacinae)) among the non-passeriforms might well have utilized a southern, rather than a northern route between Australia and the remaining world. Mayr, in commenting on Serventy's paper, tentatively considered the ratites, the platycercine parrots, and possibly the flamingos as Antarctic dispersers but left the question open. Cracraft, on the other hand, strongly supported a southern dispersal route for the ratites, megapodes, and parrots, but agreed with both Serventy and Mayr that the majority of Australian avian genera (including most of the non-passeriforms) were spawned by Southeast Asian faunas. Is this really the case, however, and what sort of reasoning and assumptions are employed to determine each family's route of dispersal between Australia and the rest of the world? The following section deals in detail with these questions.

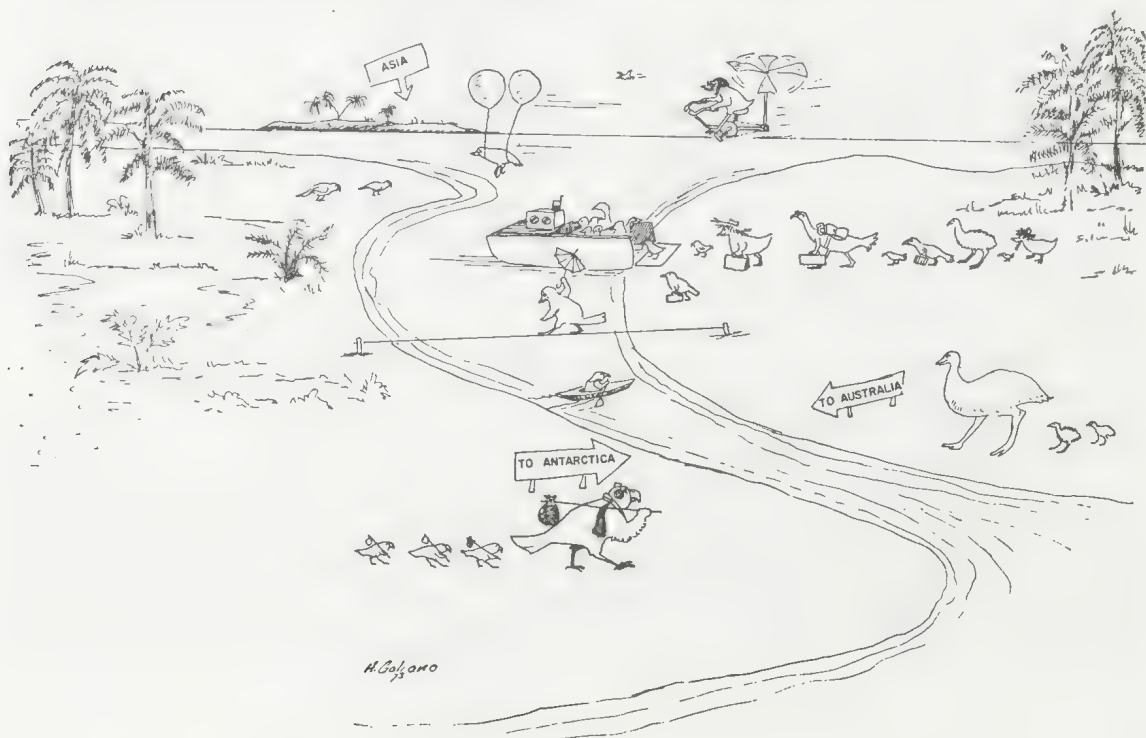
Re-evaluation of Probable Immigration Routes Into Australia: Assumptions, Reasoning, and Data

Zoogeography is often not a very satisfying endeavour owing to the frequent uncertainty of conclusions one is able to reach concerning areas of origin and early radiation of certain organisms. Despite this, however, many workers have attempted to understand the distributional histories of organisms including birds, although



Fig. 9—(A) Cartoon expressing the classic ideas concerning origin of the Australian avifauna, eloquently detailed by Mayr (1944a-b); (B) cartoon depicting an additional component

that together with Mayr's ideas may have been important in shaping the composition of Australia's bird fauna.



others seriously question many of the criteria utilized in such attempts (Rotramel, 1973, among others). The following section summarizes briefly assumptions and reasoning utilized by ornithologists and zoogeographers who have tried to determine origins of elements comprising the Australian avifauna. In addition, it outlines assumptions employed in this paper to re-evaluate the immigration and emigration pathways of all the non-passeriform families, presents pertinent historical, distributional, and diversity data for each family considered, and briefly outlines the reasoning employed in the determination of the dispersal route(s) utilized by each Australian group between Australia and the remaining world.

In his treatise on zoogeography, Darlington (1957) outlined several working principles and a number of practical clues used in determining the area of origin of different organisms including (1) diversity, (2) degree of differentiation (including degree of endemism), (3) extent of area inhabited (whether restricted or widespread), (4) continuity of area inhabited, (5) distribution of related, competing, and associated families, and (6) fossil record. How much weight to give each of these clues, particularly in cases where information is limited, was not made clear. Similarly, if some data are available for each clue category, it was not made clear which clue or clues had priority over others if multiple interpretations were possible. Darlington suggested that degree of differentiation (clue 2) should have priority over diversity (clue 1), in fact that information pertinent to the remaining clues (clues 3, 4, 5, 6) could be used to question the significance of diversity. He quite appropriately pointed out that high diversity in an area might not only signal the long history of a group there, but might also be due to a number of other factors such as the size and diversity of the environment inhabited (i.e. number of different habitats available), and the amount of competition a group encountered from other organisms during its history in an area. To this list Keast (1972) added such factors affecting group diversity as size of total area inhabited, topographic diversity, percentage of area within the tropics, total latitudinal range on continent, vegetational

composition of continental flora, and history of connection to other land masses. Darlington further stressed other problems peculiar to deciphering avian zoogeography including the (1) rapidity with which an avian taxon can disperse, thus obscuring the direction from which it came; (2) possibility of contemporaneous multiple dispersals; (3) rarity of avian fossils; and (4) lack of understanding of the significance of non-breeding ranges of migratory birds. However, after so carefully and precisely outlining these assumptions and clues, most were not evaluated when Darlington individually considered a number of "dominant" avian families; instead diversity and endemism were usually the only clues considered. Darlington's judgement on the relative significance of these few clues was not consistent; on the one hand he believed that the Phasianidae originated, or at least underwent a major radiation, in the Oriental region based on their great diversity there⁶ (in comparison to its low diversity elsewhere), but was unwilling to readily accept the equal probability that the parrots originated or underwent an early radiation in Australia based on the same type of distributional and diversity information.⁷ Besides pheasants and

⁶ "It [the Phasianidae] is the first large family of this survey which shows an apparent pattern of radiation from one main center, the Oriental Region. The true pheasants, jungle fowls, and peacocks are almost all in the Orient, and from there the ancestors of *Afropavo* (the Congo Peacock), and of the guinea fowls may have reached Africa; the ancestors of the grouse (Tetraoninae) may have gone northward and around the northern part of the world, eventually differentiating most in North America; and the quails may have radiated over the whole world, with a secondary evolution center in southern North America. The fowl-like birds *probably* [italics mine] have relatively low powers of dispersal, so their present distribution may reflect something of their early history . . ." Darlington (1957, p. 270).

⁷ "Parrots . . . are almost equally numerous in species in Old and New Worlds but are much more diverse in the former, all the New World forms belonging to one of the several Old World subfamilies; this suggests an Old World origin of parrots. But this does not carry the analysis far enough. It is only in the Australian Region and adjacent island areas that parrots occur in great diversity. Elsewhere in the Old World parrots are relatively few and all belong to one subfamily, the same one that is in America. Does the unique diversity of parrots in the

parrots, Darlington examined several other avian groups that occur in Australia (Anatidae, Falconiformes, Strigiformes, Ardeidae, Charadriidae, Scolopacidae, Rallidae, Cuculidae, Caprimulgiformes, Apodidae, Alcedinidae), attempting to determine their centres of origin and distributional histories, but could reach no further firm conclusions for any other non-passeriform group. He believed that most of the groups which he considered were old, had complex distributional histories, and that areas of origin as well as early patterns of radiation could not be determined. He noted that the Caprimulgiformes (nightjars, frogmouths, and allies) probably had experienced three major radiations, one in the Australian-Oriental area (Podargidae, Aegothelidae), another in tropical America (Nyctibiidae, Steatornithidae), and a third in an undesignated area that produced the Caprimulgidae, but he was non-committal about what dispersal paths had been employed during this tripartite diversification. It is with this background of uncertainty about the dispersal histories of birds that Darlington made the following statement: "Almost all the ascertainable relationships of Australian land birds are toward Asia. The few supposed African relationships, for example that of the honey eaters with *Promerops* of South Africa, are doubtful, and there is no sure, direct relationship between any Australian and South American land birds" (1957, p. 262). Thus with this statement and others regarding the origins of the parrots and pigeons, Darlington emphasized the "Asiatic" character of the Australian avifauna, essentially agreeing with Mayr's ideas.

Mayr's (1944a-b) reasoning, that most Australian birds were derived from Oriental forms, relied heavily on the two observational assumptions that (1) the Australian avifauna more closely resembled that of the Oriental region than that of any other area and (2) during the history of birds, Australia had re-

mained in its present geographic position, with colonization slowly accelerating as more of the Malay Archipelago emerged during the Cenozoic. With such a foundation, Mayr's conclusion (that Australia's avifauna consisted of several different "waves" of northern colonists) was quite reasonable. However, as a previous section of this paper has established, present geological evidence strongly suggests that Australia has been anything but stable during the history of birds, having drifted as much as 30-50° of latitude from an Eocene connection with Antarctica nearly to its present position by the late Miocene. Thus Mayr's second assumption is seriously challenged. If his first assumption is re-examined, although most certainly true, it could have resulted from at least two types of faunal interchange, i.e. (1) Australia receiving most of its avifauna from Asia or (2) the most recent biotic interchange between Australia and the rest of the world being with Asia. If the latter is the case, similarities between Asia and Australia would have resulted from a mixing of the two faunas, not a one way immigration from Asia. Because of the present lack of understanding of avian distributional histories, however, the conclusion that Asia spawned most of Australia's avifauna seems premature, a conclusion far too specific for the limited data available.

Serventy (1972, 1973), accepted the recent consensus of geologists supporting continental drift and re-examined the old, endemic elements in Australia's avifauna, attempting to point out the closer relationships of some Australian birds to South American rather than Asian forms. His acceptance of ratite monophyly (as most recently supported by Bock, 1963; Meise, 1963; Parks and Clark, 1966; Sibley, 1960) allowed him to support strongly a southern dispersal route for this group, and along with additional data, led him to state: "May not some of the older elements of the present Australasian fauna have reached Australia via Africa and Antarctica during the earlier stages of Gondwanaland?" Serventy did not extend his considerations to other, less unique Australian bird groups, because he believed they had immigrated from Asia due to their lack of close similarity to South American forms.

Australian Region reflect place of origin, or withdrawal of some groups of parrots from other parts of the world, or local radiation? I cannot answer this question, but it seems to me that parrots need not have originated in the Australian Region . . ." Darlington (1957, p. 271).

Cracraft (1972, 1973) likewise assumed that continental drift had occurred during the Mesozoic and Cenozoic (in fact he presented a review of continental drift literature) and attempted to elucidate the dispersal histories of avian taxa based primarily on phyletic relationships of those taxa (using a method discussed by Hennig, 1966; Nelson, 1969; and others). He emphasized that all other clues regarding origin of avian groups should be subordinate to phyletic clues, but then noted how pitifully poor present understanding of phyletic relationships was for most avian families and thus, I assume, how little is understood of original dispersal routes if that information is derived from phyletic studies. He discussed those few groups whose relationships he believed were best understood, including taxa with Australian histories: penguins (Spheniscidae), ratites, galliforms (including Megapodiidae), parrots (Psittacidae), pigeons (Columbidae), and cuckoos and allies (Cuculiformes) among the non-passeriforms. Yet with this limited consideration as a basis, he was willing to conclude in another paper (Cracraft, 1972, p. 173, as well as 1973) that "the vast majority of Australian families undoubtedly have relationships to Asian families and therefore can be supposed to have come from the north. This includes *most non-passerines* [italics mine] and all oscines." Cracraft, like Serventy, did not present data that would support such a statement, and thus presumably accepted much of the reasoning previously articulated by Mayr and Darlington. Unfortunately, all of these workers have not stated the important point that similarity of the Australian and Asian avifaunas could well be due to a two-way, not just a one-way, exchange of old endemic faunas, and that present-day avifaunal similarity need only signal the latest, not necessarily the sole, episode of interchange between Australia and the rest of the world. Why not investigate the Australian nature of the Oriental avifauna as well as the Asian nature of the Australian avifauna? It, also, should be realized that because linkage between Australia and other southern continents was broken during or before the Eocene, birds on any of these gondwanic continents today have had ample

time to evolve quite separately and diverge from one another. Relationships between living forms that might be used in support of such an early Tertiary dispersal route should thus be sought at higher taxonomic levels, not specific and generic.

In this paper a number of assumptions will be made and clues used in an attempt to decipher the dispersal history of Australian avian families. Assumptions include:

- (1) the geographic arrangement of continents has been continually altered throughout the history of birds and quite profoundly in the positioning of Australia during the Cenozoic (i.e. Australia has drifted from an early Tertiary position adjacent to Antarctica, perhaps as much as 30-50° of latitude northwards), nearing its present position by the late Miocene;
- (2) if the geographic position of a continent relative to others has changed during the history of a group of organisms, then faunal composition on any one continental mass may reflect several episodes of exchange with other geographic areas; those areas most recently in contact or closely apposed to one another should be expected to exhibit the greatest faunal similarity.

With these assumptions the practical clues examined in an attempt to determine the dispersal routes to and from Australia utilized during the history of any one avian family include:

- (1) phyletic relationships of the family to others (accompanied by distributional and degree of differentiation data for "other" families);
- (2) fossil history of family, worldwide;
- (3) degree of endemism of family both within and outside of Australia (see figure 5);
- (4) diversity of family both within and outside of Australia (see figure 5);
- (5) nature of distribution: cosmopolitan, pantropical, restricted; continuous or segmented.

How each of the above clues are interpreted in the following study needs brief explanation:

Phyletic relationships. If a group (or groups) can be identified as being closely related to a family with Australian representatives, and information is available concerning intragroup phyletic relationships, then those data will sometimes favour one dispersal route over another between Australia and the rest of the world, although not always allowing resolution of the direction of movement along that route. An explanation of the observed distribution of the group members (including the Australian taxa) attempts to determine the minimum number of dispersals necessary (see Nelson, 1969, for excellent discussion of this procedure) to produce the present array of birds with the constraints imposed by understanding of phylogenetic relationships and knowledge of Mesozoic and Cenozoic paleogeography. Such explanations, however, offer only "parsimonious" first approximations that may well be refined, and perhaps found to be decidedly more complex, if understanding of the phylogeny of certain avian groups is improved and/or a more geographically and temporally complete fossil record of birds materializes in the future. Recent and fossil material are of equal importance when constructing phylogenies, each limited by incompleteness of specimens (or study thereof) or of geographic representation. Geographic position of the most primitive taxa (especially if based on living forms alone) is *not a priori* assumed to be indicative of the centre of origin or early radiation of a group but must be examined in light of the distributional patterns of other more primitive and advanced members of the group.

Unfortunately, this clue is of limited use because of the poor understanding of phylogenetic interrelationships of many of the non-passeriform taxa. This is well demonstrated by diversity of opinions expressed today concerning interfamilial relationships of birds, many of which are cited in the following section.

Degree of endemism and diversity. Darlington (1957) has posed some serious objections to the use of endemism and diversity (see previous section of this paper), but in this study, such clues do seem helpful in two

extreme cases, i.e. where (1) a family is highly diverse, having a large number of endemic genera/subfamilies in Australia but is unrepresented or has only a scant record elsewhere and (2) a family is highly diverse outside Australia but is represented in Australia by a single genus or species, often conspecific with extra-Australian populations.

Case 1 may represent a group that has had a long history in Australia and just recently emigrated elsewhere, especially if the extra-Australian forms are closely (conspecific or at the most congeneric) related to Australian taxa. The high diversity and endemism in Australia cannot be explained by that continent's greater environmental diversity in comparison to that of its nearest continental neighbour today, the Palearctic-Oriental region. Certainly a greater topographic and climatic diversity, a decidedly greater land area (ca. 3 million miles² in Australia; ca. 21 million miles² in the Oriental-Palearctic; and ca. 33 million miles² in the Old World when Africa is included (Golenpaul, 1960)), as well as a greater tropical land area characterizes the Palearctic-Oriental Realms when compared with the Australian (excluding New Zealand). As previously mentioned (also see below), the effect of differential competition encountered by an avian group in either area cannot be measured and remains unknown in this consideration. Thus original entry of groups in this category into Australia via an Antarctic dispersal route should be considered a possibility along with an Indomalaysian route. If the extra-Australian forms are quite distinct (although few in number), however, the situation may be more complex and will be discussed further under each family affected.

Case 2 apparently represents the opposite extreme, a group that has only recently arrived in Australia and has not yet differentiated to any marked degree. In this case the Indomalaysian or transoceanic route is most probable paths of original entry.

Of course, these two cases represent the extremes of a spectrum of possibilities; many avian families are moderately diverse, with many endemic taxa in several areas of the world, including Australia. Unless other data

are available, it may be impossible, as Darlington (1957) has suggested, to determine the most probable route of initial entrance for these families at present.

Nature of distribution. Distributional clues have been used as discussed by Darlington (1957), i.e. the continuity or discontinuity of an area inhabited by a particular group can be used to determine if a group has recently or long ago invaded an area, where a disjunct distribution is indicative of a group that has invaded long enough in the past to have experienced fragmentation into disjunct populations separated by considerable distances.

Two other clues that Darlington (1957) employed in his considerations of avian zoogeography are not particularly useful when considering the origin of the Australian avifauna because of the total lack of or rarity of data for each: the distribution of "competing" families and the composition of fossil avifaunas.

In the former case I know of no careful and sufficiently broad-based studies designed to determine what avian families (or for that matter what other organisms, not just birds) are "competing" with certain Australian taxa both within and outside of Australia. How much (or how little) competition a taxon encounters in different geographic areas may well be the primary factor accounting for differential diversity in certain areas, but how can this be recognized and measured? Darlington (1957) very appropriately pointed this problem out, and it should be kept in mind to temper all conclusions regarding location of early centres of radiation, as well as antiquity of families in certain areas, particularly in the case of Australia where the early Tertiary fauna may well have been impoverished and unbalanced and where there is no fossil record to confirm what groups were actually there.

The fossil record, also, is not particularly helpful at present in determining what dispersal route was used by birds present in Australia during the Cenozoic because of the incompleteness of the Paleogene record in Australia (see Table 3), South America (Pascual and Rivas, 1971), and Southeast Asia. Only Europe and to a lesser extent North America (mid to

late Cenozoic in particular) have produced sufficient fossil material to allow partial reconstruction of Cenozoic avifaunas. To some extent, early Tertiary European avifaunas can be used to suggest what avian taxa might have simultaneously lived in Southeast Asia, but such would only be extrapolation in need of confirmation, since barriers to overland dispersal may well have separated the two areas during parts of the Tertiary (see Szalay and McKenna, 1971; McKenna, 1972a). Just because such early Tertiary faunas are not presently known, however, one should not condemn the value of fossils for the future. Were the records more complete, particularly in South America and Australia, questions regarding the antiquity of many groups in these areas could be answered, as could those concerning which dispersal route between Australia and the rest of the world was most likely for those groups. Were the record more complete, it could be used to evaluate parsimonious conclusions based solely on phyletic relationships and distribution of modern taxa, which may be gross oversimplifications of reality.⁸ In making such a statement, I am not advocating a cessation of research on avian phylogeny, which I think can

⁸ A group that well exemplifies such oversimplification by parsimonious arguments based on the living fauna alone is the mammalian order Perissodactyla represented by the tapirs (tropical America, Southeast Asia, and Indonesia), the rhinoceroses (Africa, eastern Asia, and Indonesia), and the horses and allies (central and eastern Asia and Africa) in the modern fauna (Walker, 1964). Of these living forms the tapirs are the most primitive and the horses most advanced or derived (Simpson, 1945). Thus the most parsimonious explanation of origin and dispersal of this group would require an Old World origin of the equids and the rhinoceroses and an Old or New World origin of the tapirs. The fossil record, however, indicates the "reality" of perissodactyl dispersal was far more complex than the modern record intimates. A wide variety of equids and rhinoceroses as well as a number of now extinct perissodactyl groups inhabited North America and Europe, as well as those areas now inhabited by this order at various times during the Cenozoic. Without necessarily altering the hypothesized phyletic relationships of the living perissodactyls, the fossil evidence certainly increases the possibilities for area of origin and early radiation of both the horses and rhinoceroses, challenging the specificity implied by the original parsimonious argument.

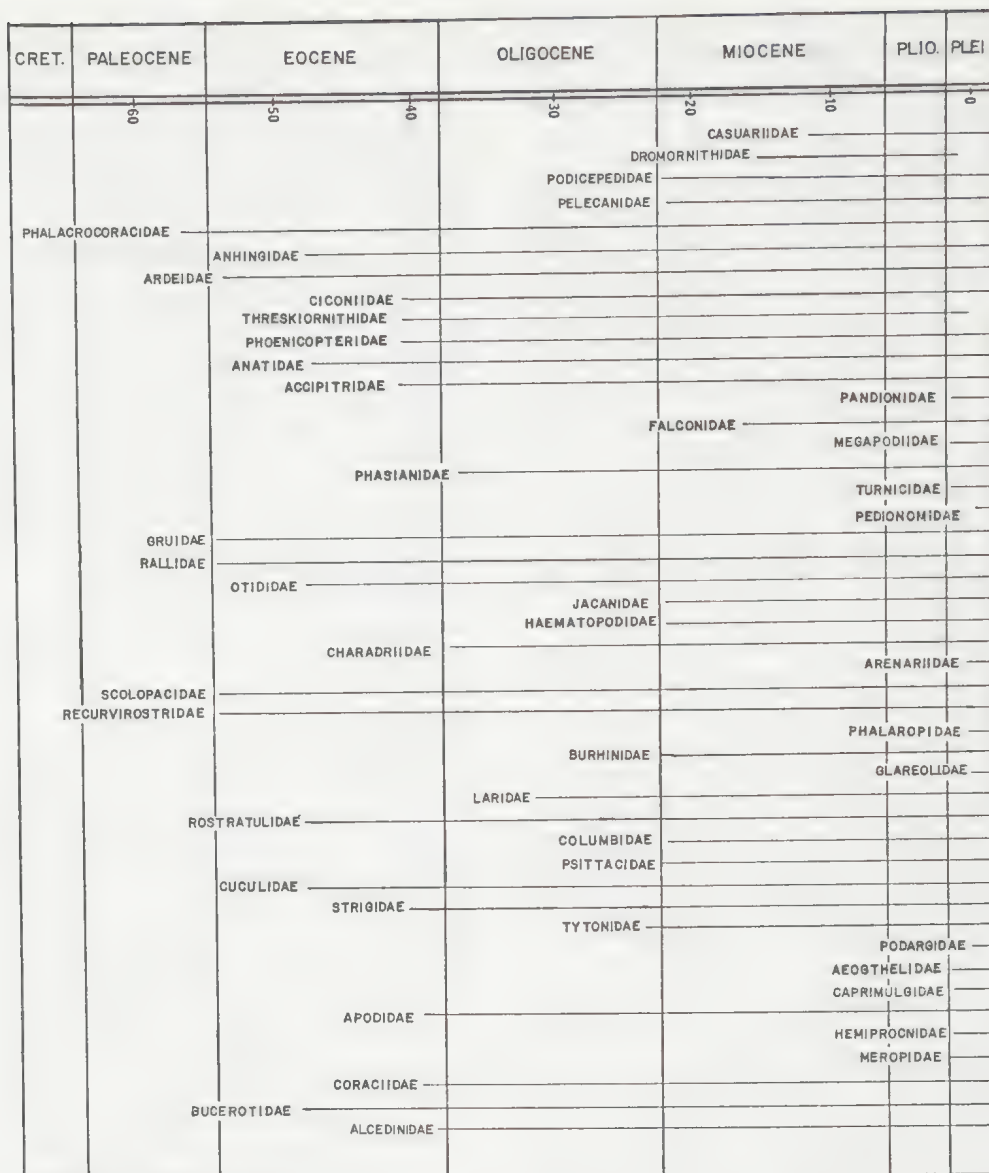


Fig. 10—Geologic ranges (world-wide) for those non-passeriform avian families represented in the Cenozoic of Australia. Horizontal axis calibrated in millions of years, in general following Berggren, 1969, 1971.

only help in understanding of avian distribution, but I am criticizing those who would condemn the fossil record as a useless, even misleading item of information for zoogeographic considerations. A good fossil record combined with data from the living fauna and continental reconstructions for the Mesozoic and Cenozoic, on the contrary, can offer alternatives (and often a closer estimate of reality, even if that

estimate is more complex) that cannot be confirmed by, or deduced from, the modern avifauna alone (see Cracraft and Rich, 1972, concerning the early radiation of the Cathartidae in Europe; also Nelson, 1969).

Despite the rarity of avian fossils in most parts of the world, the palaeontological record is important to this study in one way. It demonstrates that at least twenty of the forty-six avian families (see figure 10) that make up the Cenozoic avifauna of Australia had probably differentiated by the Eocene (data mainly from Brodkorb, 1963, 1964, 1967, 1971a) and thus

could have utilized the Antarctic dispersal route to initially disperse between Australia and the remaining world.

Summary of Phyletic Relationships, Diversity, Endemism, Distribution, and Palaeontological Record of Avian Families Having Australian Representatives

Using the five clues (phyletic relationships, diversity, endemism, distribution, fossil record) stressed in the previous section, an attempt is made in this section to determine for each avian family with a Cenozoic record in Australia what the most probable route of entry has been. Palaeontological data are given to emphasize which families are known to have differentiated by the early Tertiary, thus indicating the real possibility that the Antarctic dispersal route could have been used. Data for each family are presented in the following order: technical and common names; temporal range (both for world and Australia; if coincident only one range listed); geographic range; total number of living and fossil genera (if different from following category); total number of living and fossil genera in Australia-New Guinea; geographic area of greatest diversity; geographic area of greatest endemism (at generic, sub-familial levels); phyletic relationships to other avian families. A brief analysis follows each set of data for every family and attempts to establish which dispersal route, Antarctic and/or Indomalaysian, has been used. In many cases both routes may have been utilized at different times during the history of an avian family while in other cases one route seems more probable. In several cases, a choice of routes cannot be made based on available data.

The familial classification employed follows that of Peters (1931, 1934, 1937, 1940, 1945) with synonymies of the Mayr and Amadon (1951) and the Brodkorb (1963, 1964, 1967, 1971a) classifications also listed. Generic assignment to each family follows Peters (see above) except where modified by Bock (1956), Woolfenden (1961), Brown and Amadon (1968), Rand and Gilliard (1968), Sibley and Frelin (1972), Rich (1973) and Condon (in press). Data on diversity and endemism were derived primarily from Peters and Condon

(see above), palaeontological data from Brodkorb (see above and 1971b) and Olson (1974), and phylogenetic information from Brodkorb, Mayr and Amadon, Storer (1960, 1971), Woolfenden, Brown and Amadon, Bock, and Sibley and Ahlquist (1972). The latter reference summarizes most of the important works on avian phylogenetic studies and will not be duplicated here.

Casuariidae (Dromiceidae, *Casuariidae* of Mayr and Amadon, 1951; Brodkorb, 1963; *Casuariidae* of Sibley and Frelin, 1972). Emus and cassowaries; Miocene-Recent; *Dromaius* restricted to Australia, *Casuaris* to Australia, New Guinea, and some Pacific islands; two genera in family, *Dromaius* and *Casuaris*; greatest endemism and diversity in Australia; nearest extra-Australian relatives, elephant birds and rheas-ostriches, not moas and kiwis; nearest relatives, the dromornithids (Rich, 1973).

The emus and cassowaries form a unique, quite distinct and moderately diverse ratite group in Australia whose nearest extra-Australian (New Guinea and Southwest Pacific included) relatives occur in South America and Africa (see Rich, 1973; Cracraft, 1973; Sibley and Frelin, 1972; Jehl, 1971; Glenny, 1965; Sibley, 1960). The family is also present, but neither as diverse nor endemic, in New Guinea and on some southwest Pacific islands. The only ratite known from Asia, the ostrich (*Struthio*), first recognized in Europe and Africa in the late Miocene (Rich, 1972), is far too specialized to have given rise to the Australian ratites, however. Casuariid differentiation had occurred in Australia by the Miocene, and therefore a Paleogene or earlier differentiation is necessitated. More advanced ratites were present in South America during the Eocene (Brodkorb, 1963; Rich, 1973; Cracraft, 1973), and thus forms that could have been ancestral to Australian ratites must have differentiated even before, and an early dispersal of this group across a southern route must be considered a possibility.

Dromornithidae. Mihirung birds; Miocene-Pleistocene (presently extinct); restricted to Australia; 5-6 genera, including *Genyornis* (Stirling, 1896; Stirling and Zietz, 1896; 1900;

1905; 1913), *Dromornis* (Owen, 1872; 1874; 1879a-b) and 3 new genera (Rich, 1973); nearest extra-Australian relatives probably elephant birds (*Aepyornithidae*), rheas (*Rheidae*); nearest relatives the *Casuariidae*.

The Mhirung Birds (Rich, 1973) or "giant emus" appear to be most closely related to the *Casuariidae* (Rich, 1973) and both in turn are closer morphologically to the more primitive elephant birds and more advanced rheas-*ostriches* than to the moas-kiwis (Rich, 1973). The same biogeographic arguments that are valid for the *casuariids* hold for the *Dromornithidae*, and thus an Antarctic route needs to be considered a possibility for the ancestors of both groups.

Podicipedidae. Grebes; Miocene-Recent; Pleistocene-Recent in Australia; cosmopolitan distribution; 6 genera in family (2 extinct); 1-3 genera (*Podiceps*, ?*Poliiocephalus*, ?*Tachybaptus*) having cosmopolitan distribution, with remaining genera in New World; nearest extra-Australian relatives (at the family level) not certain, perhaps the loons (*Gaviidae*) with an entirely Holarctic distribution (first fossil occurrences Paleocene of Europe, Oligocene of North America), *Enaliornithidae* (extinct, Cretaceous of England), *Lonchodytidae* (extinct, Cretaceous of North America), *Baptornithidae* (extinct, late Cretaceous of North America), *Charadriiformes*, *Spheniscidae*, *Pelecaniformes*, *Procellariiformes*, or *Anseriformes*.

Three species of grebes (*Podiceps ruficollis*, *P. cristatus*, and *P. poliocephalus*) are present in the recent Australian avifauna. The first two have ranges extending into most of the Old World, and only *P. poliocephalus* is endemic to Australia. For a number of reasons initial entrance via southward dispersal along the Indomalaysian route seems most probable: (1) greatest generic diversity within the family as well as specific diversity within *Podiceps* is in the New World; (2) probable nearest relatives to the family occur in Holarctica (including North America); and (3) the family is represented by only one genus in Australia, a genus that is not endemic or particularly diverse there.

Pelecanidae. Pelicans; Miocene-Recent; one genus (*Pelecanus*) with world-wide distribution

and a second fossil genus, *Liptornis* (mid-Miocene, South America); nearest extra-Australian relatives probably within the *Pelecaniformes*: Lanham (1947) believed the *Phaethontidae* and *Fregatidae*, with recent pantropical distributions, were the most primitive members of the *Pelecaniformes*, and thus more primitive but closely related to the *Pelecanidae*; other possible close relatives are the fossil families *Odontopterygidae* (Eocene of England), *Pseudontornithidae* (Miocene of Brazil or Germany?), Miocene of North America, Pliocene of New Zealand), *Pelargornithidae* (Miocene of Europe), *Cladornithidae* (Oligocene of South America), *Cyphornithidae* (Miocene of North America).

More diverse in the past (2 genera in the Miocene), the pelicans are represented by a single genus in the living avifauna that is most varied in the Old World (Africa-Europe-Asia). One species occurs in, and is endemic to, Australia, as is another in the New World (out of a total of seven species). Because of the lack of distinct endemics (at the generic level) restricted to Australia and/or Australia-Old World and the low diversity of the genus *Pelecanus* in Australia, entrance via the Indomalaysian route or even oceanic dispersal is more probable. Also, if the *Pelecanidae* really were derived from forms similar to tropic birds and frigate birds with tropical distributions, Indomalaysian dispersal would be favoured.

Pelecanus tirarensis, the mid-Miocene form from interior Australia, may well be close to the ancestral form that first entered Australia (as it neared Southeast Asia) and gave rise to the living *P. conspicillatus*.

Phalacrocoracidae. (Phalacrocoracinae of Mayr and Amadon, 1951). Cormorants; Paleocene-Recent; Miocene-Recent in Australia; family cosmopolitan; 2-3 living, 4 extinct genera including *Graculavus* (Paleocene of North America), *Actiornis* (Eocene of England), *Pliocarbo* (Pliocene of Europe), and *Plotopterum* (Miocene of North America); one genus, *Phalacrocorax*, with a cosmopolitan distribution, only member of family in Australia; fossil record of *Phalacrocorax* extends into early to mid-Oligocene; living members of family equally diverse and endemic in New and Old Worlds; nearest relatives the specialized *Anhingidae* (see below); closest relatives of the

cormorants-anhingas possibly contained in the suborder Sulae (see Brodkorb, 1963; in agreement with Lanham, 1947) including the Eloptrygidae (Cretaceous-Eocene of Europe) and the Sulidae (first occurrence in the Oligocene of Europe, Miocene of North America; cosmopolitan at present).

Although *Phalacrocorax carbo* suggests by its cosmopolitan distribution that an Indomalaysian or oceanic route has been used most recently by the cormorants, direction of movement along that route is not certain. The Phalacrocoracidae are quite an old group, first recognized in the late Mesozoic/Paleogene of North America and Europe, as is *Phalacrocorax*, which is first known in the mid-Oligocene. Unfortunately, none of the practical clues used in this study favour one route over another. Phyletic relationships of the phalacrocoracids, including *Phalacrocorax*, to other birds (other than to the more specialized tropical anhingas) are not well understood, diversity and endemism are about uniform the world over, and distribution is nearly continuous along continental margins and somewhat inland over most of the world except in the far north and far south. To further complicate matters, the cormorants are not restricted to fresh-water environments, and oceanic dispersal could easily have played an important part in their dispersal with regard to Australia.

Thus, with present evidence, it appears impossible to determine the route initially used by the cormorants between Australia and the rest of the world.

Anhingidae. (Anhinginae, Mayr and Amadon, 1951). Anhingas, darters, or snake birds; ?Eocene-Recent; Miocene-Recent in Australia; 2 genera in the family (*Protoplotus*, restricted to ?Eocene of Sumatra); one genus, *Anhinga*, in Australia, has pantropical distribution; family presently with similar diversity and endemism throughout tropics of the world; nearest relatives the Phalacrocoracidae, with a cosmopolitan distribution.

The one species of anhinga (*A. melanogaster*), occurring in Australia, also extends throughout tropical Asia and tropical Africa, being distinct from the New World *A. anhinga*. A second distinct species, *A. laticeps*, was

reported from the Pleistocene of Australia (DeVis, 1905; confirmed by Miller, 1966a). Because of their present and past (see Rich, 1972, 1974) restriction to warm, wet climates, an Indomalaysian dispersal route seems most probable. At no time during the late Mesozoic or early Tertiary could the Antarctic route have had a climate that was more equable than temperate. The warm, humid tropical climate presently characteristic of some parts of northern Australia and New Guinea is a mid to late Tertiary innovation as the Australian plate drifted into the lower latitudes. The occurrence of *Protoplotus*, thought to be an early member of the Anhingidae (Lambrecht, 1931), in Paleogene sediments of Sumatra does not contradict the above conclusion.

Ardeidae. Herons and allies; early Eocene to Recent; no fossil record in Australia; family cosmopolitan; 27 living, 8 extinct genera; 9 living genera in Australia-New Guinea, none of which are endemic; one-third of genera in family with cosmopolitan distribution; greatest diversity and endemism in both New and Old Worlds, similar in both areas; nearest relatives perhaps the cosmopolitan Ciconiidae (Ligon, 1967, would disagree) (first appear in Eocene in circum-Mediterranean area; Oligocene in South America; Miocene in North America; Pliocene in Asia; Pleistocene in Australia) or the nearly cosmopolitan Threskiornithidae (first occur in Eocene in Europe; Miocene in South America; and Pleistocene in North America, Africa, and Australia).

Hérons and allies have had a long history, the family certainly being differentiated by the early Tertiary (Eocene of Europe and North America; Eocene-Oligocene of Africa). The most recent movement of this group has been across the Indomalaysian route as exemplified by the cattle egret (*Bubulcus* = *Ardeola*) that has reached Australia from Asia in the last few years (Crosby, 1972). The remaining ardeids, except for *Zonerodius* (restricted to N.G.-SW Pac.), are all wide ranging genera, most of which are decidedly more diverse outside of Australia. Diversity and endemism of the family is about equal in both the New and Old World while low in Australia, all of which suggests that the Ardeidae dispersed southward from Palearctica into Australia

and/or may have utilized an oceanic route.

Ciconiidae. Storks; Eocene-Recent; Pliocene-Recent in Australia; family cosmopolitan except for New Zealand; 11 living, 9 extinct genera only one of which (*Xenorhynchus*) is known in Australia; greatest diversity and endemism of family in Old World (Africa and Asia in particular, although three genera known in New World); nearest relatives probably Ardeidae or Threskiornithidae (see above), both of which have recent distributions that are nearly, if not, cosmopolitan and long fossil records (Eocene to Recent), or Cathartidae (Ligon, 1967).

Owing to the low diversity (one endemic genus with one species) of this family in Australia and its high diversity and endemism in neighbouring Asia (as well as the remaining Old World), entrance of the Pleistocene-Recent members of this group from Southeast Asia via the Indomalaysian route seems most probable.

Threskiornithidae. (= Plataleidae of Brodkorb, 1963). Ibises and spoonbills; Eocene-Recent; Pleistocene-Recent in Australia; 17 living, 3 extinct genera; 3 living genera in Australia; family cosmopolitan; greatest diversity and endemism in Old World with 7 genera known from New World; nearest relatives, Ciconiidae or Ardeidae, both with nearly or completely cosmopolitan distributions and long fossil histories (Eocene to Recent).

The three genera of threskiornithids represented in Australia have either cosmopolitan (*Plegadis*) or wide ranges in the Old World (*Platalea*, *Threskiornis*), and none is endemic to, or any more specifically diverse in, Australia than elsewhere. Because of such low diversity and the lack of endemic generic or suprageneric taxa in Australia at present, an Indomalaysian route for dispersal of those forms in Australia appears most probable.

Phoenicopteridae. Flamingos; late Eocene-Recent; Miocene-Pleistocene in Australia (presently extinct); nearly cosmopolitan; 3 living, 3 extinct fossil genera (*Elornis*, Eocene-Oligocene of Europe; *Tiliornis*, Oligocene of South America; *Phoeniconotus*, Miocene of Australia); no living phoenicopterids in Australia but an endemic genus (*Phoeniconotus*) and *Phoenicopus* present during Miocene, *Phoeniconaias* in the late Pliocene, while *Phoenicop-*

terus persisted into Pleistocene; greatest diversity of family presently in South America and Africa but, when fossils considered, also in Australia; nearest relatives the Palaelodidae (Miocene-Pliocene of Holarctica), Agnopteridae (Eocene-Oligocene of Europe); Telmatidae (early Eocene of South America), Sclaiornithidae (early Paleocene of Europe), Torotigidae (late Cretaceous of Holarctica), and more distantly the Ciconiidae and Threskiornithidae, and probably the Anseriformes (Delacour and Mayr, 1945; Hopkins, 1949) and Ciconiiformes (Mayr and Amadon, 1951; Glennys, 1955; Sibley, 1960) (both orders, Mainardi, 1962, 1963) all of which have cosmopolitan ranges but differing degrees of diversity and endemism in different parts of the world.

Although not members of the living avifauna of Australia, during the Tertiary the flamingos formed a moderately diverse group on that continent, including one endemic genus (*Phoeniconotus*). During the Pleistocene, this group became extinct in Australia (Miller, 1963b), but survived in other parts of the world in varied climatic zones from tropical to temperate. All of the Australian genera, except *Phoeniconotus*, are also represented in the Old World (*Phoeniconaias* restricted Africa), or over most of the world in tropical to temperate climates (*Phoenicopus*). At present the family does not occur in Southeast Asia and the East Indies, being restricted further west in Eurasia and Africa in the Old World. Because the family had differentiated by the early Tertiary in both Europe and South America, and is at present equally diverse and endemic in both geographic areas, both the Indomalaysian and Antarctic dispersal routes must be considered seriously. The Indomalaysian or an oceanic route has probably been utilized most recently, accounting for the Pliocene-Pleistocene similarity at the generic level of *Phoenicopus* (in fact Miller (1963b) suggested specific synonymy with *P. ruber* in the Pleistocene) as well as close resemblance of the Australian Pliocene *Phoeniconaias* and the same genus occurring in Africa today. Whether this was brought about strictly by a northward movement during the Miocene (or slightly before) in the case of *Phoenicopus*

(first recorded in Europe during the early Miocene) and then or perhaps later in the case of *Phoeniconaias*, or whether movement was southwards from Eurasia, or both (different for each genus), is at present unclear. Since the extinct European Tertiary forms *Elornis* and *Tiliornis* have not been thoroughly re-examined since the late 19th century, it is uncertain how closely either is related to the Recent and other fossil genera from Europe, Africa, Australia, and the New World. At present, then, which was the initial route of dispersal between Australia and the remaining world has not been determined.

Anatidae (including *Anseranatidae* of Woolfenden, 1961). Ducks, geese, swans; Eocene-Recent; Miocene-Recent in Australia-New Guinea; 51 living, 23 extinct fossil genera, 13 genera in Australia-New Guinea of which *Anseranas*, *Stictonetta*, *Malacorhynchus*, *Cereopsis*, *Chenonetta*, and *Biziura* are endemic; family cosmopolitan and only slightly more diverse in Old World than elsewhere; many genera with Holarctic distribution; nearest relatives probably the *Anhimidae* (screamers), presently restricted to South America.

Entrance of the many different groups of *Anatidae* into Australia has probably been complex, possibly involving both the Antarctic and the Indomalaysian routes. Differentiation of the family occurred early, at least by the Eocene and probably earlier. The most closely related family to the anatids is the *Anhimidae*, present only in South America today with a Pleistocene record on that continent. In addition, many anseriforms in the Australian avifauna are primitive members of the order. The magpie geese, *Anseranatidae* (Woolfenden, 1961; Johnsgard, 1961, 1962; Sibley and Ahlquist, 1972) or *Anseranatinae* of many classifications (Mayr and Amadon, 1951; Delacour, 1954), presently restricted to Australia, are anseriforms somewhat advanced over the anhimid condition but not so highly advanced as the true ducks-geese-swans (Woolfenden, 1961; Verheyen, 1953, 1955; Sibley (1960) has noted their distinctiveness from other anatids). The Cape Barren Goose (*Cereopsis*) is considered by some (Woolfenden, 1961; Johnsgard, 1961, 1962) to be the most

primitive member of the *Anserinae* (swan-geese subfamily). Others would disagree, however, and ally it with the sheldrakes (*Tadornini*) (Delacour and Mayr, 1945, 1946). *Cereopsis*, like *Anseranas*, is restricted to Australia presently, with a probable Pleistocene record of the family in New Zealand (evidencing ability of this group to cross water barriers in the past if interpretations of the New Zealand form are correct). The *Dendrocygnini* (tree-ducks) are considered more advanced toward the goose-swan condition than *Cereopsis* but more primitive in many characters than the *Cygnini* and *Anserini* themselves. Within the tribe of tree-ducks (Woolfenden, 1961) one very distinct genus, *Stictonetta*, is at present restricted to Australia, while *Dendrocygna* occurs pantropically, including Australia. The tribe is first recorded in Miocene sediments of South Dakota, first known in Australia in the Pleistocene. Frith (1964a-b), on the other hand, has allied this form with the swans and thus removed it from the *Dendrocygnini*. Since the most advanced subgroups within the *Anatidae* proper had differentiated by the end of the Paleogene, ancestors of more primitive members of the *Anseriformes* discussed above must have been present even earlier, and thus a southern dispersal of this group is a possibility. Then, too, such forms could have been relict in Australia after utilizing an Indomalaysian route or even oceanic dispersal.

The true geese (*Anserini*), are presently restricted to Holarctica, apparently never reaching Australia, while the remaining tribe of the *Anserinae*, the swans (*Cygnini*) have a nearly cosmopolitan distribution. The *Cygnini* are first known from Oligocene sediments in Europe, from the Pleistocene elsewhere. This early occurrence in Europe coupled with the group's maximum diversity in Eurasia presently and its probable derivation from a strictly Holarctic group (*Anserini*) all suggest southward dispersal via the Indomalaysian route.

Members of several tribes of the *Anatinae* (*Tadorini*, *Anatini*, *Aythiini*, *Oxyurini* of Woolfenden (1961)) including both primitive and advanced forms are present in Australia today. This subfamily was distinct at least by the late Oligocene when it was present in

Eurasia, in Africa by the early Miocene. Primitive members of the Anserinae that probably most closely resemble the common ancestor of the Anserinae-Anatinae (Woolfenden, 1961) occur in Australia (Cercopsini) and pantropically (or nearly so: Dendrocygnini).

It is interesting that one of the more primitive tribes of the Anatinae (Woolfenden, 1961), the Oxyurini (stiff-tailed ducks), is most diverse in South America (*Heteronetta*, *Nomonyx*, *Oxyura*) while Africa and Australia each have an endemic genus (Af.-*Thalassornis*; Aust.-*Biziura*), and both share *Oxyura*, the only form present in Holarctica. Such a distribution could be explained either (1) by initial use of the Antarctic and then a northward dispersal during the Miocene into Asia and across tropical southern Asia, Europe, and North Africa into the present Ethiopian realm before restriction of the tropics in the late Tertiary, or (2) by southern dispersal into Australia from southeastern Asia in the mid-Tertiary and differentiation since that time. At present it is difficult to make a choice between the two possibilities.

Other tribes of the Anatinae, however, have apparently arrived in Australia via southward movement along the Indomalaysian route. The Tadornini (sheldrakes), have a cosmopolitan distribution, but no one genus is cosmopolitan (2 endemic to South America, 1 to Africa, 1 to Eurasia, and 2 occur over most of the Old World including Australia). Low diversity and lack of endemism in Australia, as compared to that of the Old World, indicate that the group has moved south, instead of north along the Indomalaysian route.

The Anatini are also cosmopolitan, although several genera are endemic to different parts of the world including *Malacorhynchus* (whose relationships are poorly understood, R. Schodde, pers. comm., 1974) and *Chenonetta* in Australia; *Cheniscus* is endemic to Southeast Asia-Southwest Pacific-Australia-New Guinea. Diversity and endemism in the Old and New World are nearly equal, with that in Australia being extremely low when compared with the other continents. Because of such lack of diversification in Australia in comparison to the rest of the world, the history of the Anatini

there is apparently relatively short, and again Indomalaysia seems to be the only major dispersal route utilized.

The fourth anatine tribe, the Aythyiini, is represented by only the cosmopolitan *Aythya* (by one endemic species) in Australia, a genus much more diverse elsewhere in the world. The tribe is most diverse in Asia, most endemic in the Old World, and its earliest fossil occurrence is in the early Miocene of Europe. Woolfenden (1961) believed that the Mergini (restricted both at present and in the past to Holarctica) were the nearest, more primitive relatives of the Aythyiini. All these data strongly suggest that the Aythyiini entered Australia via Indomalaysia.

In summary, the entrance of the Anatidae into Australia has probably been complex and may have involved both the Antarctic and Indomalaysian dispersal routes. The most recent exchange, which is still in progress, undoubtedly involves only the Indomalaysian route.

Accipitridae. Hawks and eagles; Eocene-Recent; Miocene-Recent in Australia; family cosmopolitan; 63 living, 24 extinct genera; 17 living genera in Australia-New Guinea of which *Lophoictinia*, *Hamirostra* (all *Milvinae*), *Erithroriarchis* (*Accipitrinae*), and *Harpyopsis* (*Buteoninae*) are endemic; *Henicoperis* (*Perninae*) is endemic to New Guinea and the Southwest Pacific, *Haliastur* to Australia-New Guinea-Southwest Pacific-Asia, and *Butastur* to New Guinea-Asia-Africa; most closely related families *Falconidae*, *Pandionidae*, also with cosmopolitan distribution.

The Falconiformes is the most generically diverse order of non-passeriform birds, containing some 81 genera in the Peters (1931) classification and slightly less in that of Brown and Amadon (1968). Within this order, the *Accipitridae* is the most diverse family with more than 60 genera (63, Brown and Amadon, 1968; 68, Peters, 1931), equalled in intrafamilial diversity only by the parrots and pheasants. About twenty-five per cent of known accipitrid genera occur in Australia and come from several of the subfamilies within this family including three types of kites (*Perninae*, *Elaninae*, *Milvinae*), the fish eagles (*Haliaeetus*), the harriers (*Circinae*), and the hawks and eagles

(Accipitrinae). Conspicuously absent in this avifauna, however, are any of the primarily scavenging forms in the subfamily Gypaetinae, widespread in the Old World.

Most intriguing with regard to Australian biogeography are the milvine kites, thought to be some of the most primitive accipitrids (Brown and Amadon, 1968). Of a total of seven genera known, four occur in Australia, two of which (*Lophoictinia* and *Hamirostra*) are endemic to that continent. *Haliastur* occurs only in Australia - New Guinea - Southwest Pacific-Southeast Asia, while the fourth genus, *Milvus*, is found over most of the Old World in addition to Australia and the Southwest Pacific. The remaining three genera are restricted to the New World. Thus, the main diversity of this group occurs in the New World and Australia with only two genera of the seven reaching Southeast Asia and one reaching Europe. The fossils are consistent with the recent form with *Milvus* represented in the early Miocene of Europe and two presently extinct genera restricted to the New World. Certainly more advanced members within the Accipitridae had differentiated by the Eocene (Brodkorb, 1964), thus signalling an even earlier differentiation of kite ancestors. Such evidence suggests that an Antarctic route for entrance of the milvines should not be discounted. The Indomalaysian route is presently in use and could have been as early as the Miocene. Movement across this route, however, may just as well have been northwards from Australia, rather than southwards from Eurasia.

Elanus, with a nearly cosmopolitan distribution, represents the only member of Elaninae (also thought to be primitive accipitrids, Brown and Amadon, 1968) in Australia. Two other genera are in this subfamily, one genus endemic to the New World, and a second endemic to Africa. Owing to the cosmopolitan nature of *Elanus* and the lack of any more than specific differentiation of this widespread genus in Australia (*E. notatus*, *E. scriptus*), southward dispersal along the Indomalaysian route seems probable.

The third group of primitive accipitrids, the pernine kites, include seven genera, three of which occur in Australia: *Aviceda* (Af.-As.-

N.G.-Aust.-SW Pac.), *Machaerhamphus* (Af.-As.-N.G.-SW Pac.), and the Australian endemic *Henicopernis* (N.G.-SW Pac.). Three other genera are endemic to the New World and a fourth occurs in the Old World and the Southwest Pacific. As with the milvines, an Antarctic route for the subfamily should not be excluded from consideration, but neither should the Indomalaysian route. The subfamily is about equally diverse in Southeast Asia and Australia-New Guinea-Southwest Pacific, although *Aviceda* is much more diverse specifically in Southeast Asia than in Australia.

Only one genus, *Circus*, represents the Circinae in Australia. This genus has a cosmopolitan distribution, and is most diverse in the Old World, which suggests use of an Indomalaysian dispersal route, with birds moving southward from Asia.

The Accipitrinae are represented by seven genera in Australia and New Guinea: those with (1) a nearly or entirely cosmopolitan distribution (*Accipiter*, *Spizaetus*, *Aquila*); (2) an Old World-Australian and/or New Guinean distribution (*Buteastur*, *Hieraaetus*); and (3) a range restricted to Australia and/or New Guinea (*Harpyopsis*, *Erythrotriorchis*). More primitive members of the subfamily (Brown and Amadon, 1968), including the harriers and harrier hawks, are cosmopolitan. Members of the subfamily Circaetinae, probably most closely related to, yet more primitive than, the accipitrines are restricted to the Old World. Since the accipitrines have very similar diversities (more than ten genera each out of a total of more than 30) in South America, Africa, and Asia but has lower diversity and little endemism in Australia, an Old World origin seems most plausible for the Australian forms. The Indomalaysian archipelago may well have been the only route utilized by accipitrines now known in Australia between that continent and the rest of the world.

Pandionidae. Ospreys; Pleistocene-Recent; only Recent in Australia; one genus (*Pandion*), which has nearly cosmopolitan distribution including Australia-New Guinea; family probably most closely related to Accipitridae (Hudson, 1948; Jollie (1953) uncertain about relationships with falconiforms; Compton

(1938) allies with Cathartidae), which likewise has cosmopolitan distribution.

The osprey (*Pandion haliaetus*) is the only member of this family and has a nearly cosmopolitan distribution, but does not occur in New Zealand. Its record extends into the Pleistocene of Europe and North America but no further. Due to its widespread nature and singular lack of diversity, it might be thought of as a relatively recent development (Ricklers and Cox, 1972; Mayr, 1963). Thus, the Indomalaysian dispersal route has most probably been involved and not the Antarctic. Whether the direction of movement was north or south can be questioned, and until the relationships of the pandionids are more clearly understood, an Australian origin cannot be ruled out.

Falconidae. Falcons/caracaras. Miocene-Recent; ?Pleistocene-Recent in Australia; family cosmopolitan; 11 living, 3 fossil genera; 1 living genus (*Falco*, nearly cosmopolitan) and possibly 1 endemic fossil genus (*Plioaetus*⁹) in Australia; most closely related family, Accipitridae (also cosmopolitan in distribution) or even the Strigiformes (Sibley and Ahlquist, 1972) (Eocene-Recent, cosmopolitan).

The Falconidae, most diverse in the New World, is represented in Australia by a single living genus and possibly one endemic form, thought by most workers to be congeneric with *Falco*. *Falco* is quite diverse world-wide, with only seven species in Australia-New Guinea. Thus, it has most probably utilized the Indomalaysian route, moving southwards from Asia.

Megapodiidae. Mound builders, brush turkeys; Pleistocene-Recent; family restricted to Australia, New Guinea, and the Southwest Pacific; 7 living, 1 fossil genera; 6 living genera (2 endemic: *Leipoa* and *Alectura*) and 1 fossil (*Progura*) from Australia; family with about equal diversity and endemism in Australia-New Guinea and the Southwest Pacific; most closely related family Cracidae (curassows and chachalacas) of tropical America (Hudson *et al.*, 1966, 1969; Holman, 1964; Cracraft, 1972, 1973) although some would dispute this relationship (see refs. in Sibley and Ahlquist, 1972).

The mound-builders are galliforms endemic

⁹ Named by DeVis and needs restudy to ascertain its taxonomic position.

to Australia and the southwestern Pacific. They are thought by some workers to be primitive within this order and most closely related to the South American chachalacas (Cracidae; Cracraft, 1972, 1973; Hudson *et al.*, 1959, 1966; Chandler, 1916). Others have suggested, on the contrary, that megapodes are specialized phasianids (Clark, 1960, 1964a-b) or that cracids are more closely related to pheasants than either is to the megapodes (Sibley and Ahlquist, 1972). Providing that megapodes are actually primitive galliforms, they may be assumed to have differentiated by the Eocene (Brodkorb, 1964) because pheasants had appeared by this time. In such a case, an early southern dispersal of the mound-builders would have been a distinct possibility. On the other hand, the group could also have moved south across the Indomalaysian route and been isolated there at some time during or after the mid-Tertiary. Both hypotheses are viable but neither is more probable than the other in light of available data.

In Australia two living and one extinct (a giant Pleistocene form, *Progura* (van Tets, 1974a)) genera are endemic. Three other genera (*Megapodius*, *Telegalla*, *Aepyodius*) occur in Australia and/or New Guinea-Southwest Pacific, while *Macrocephalon* and *Eulipoa* occur only in the Southwest Pacific.

Phasianidae. (Phasianinae of Mayr and Amadon, 1951; Brodkorb, 1964). Quail, pheasants; early Oligocene-Recent; Pleistocene-Recent in Australia/New Guinea; two subfamilies—Phasianinae, restricted to the Old World and Australasia; Odontophorinae, restricted to the New World; 59 living, 8 extinct genera; 4 living genera in Australia-New Guinea, of which only *Anurophasis* is endemic (restricted to New Guinea at present but has Pleistocene record in south-eastern Australia); closely related to the Numinidae (guinea fowl, restricted to Africa presently, Pleistocene record in Europe), the Holarctic Tetraonidae (grouse, first occurs in early Miocene of North America, Pleistocene in Europe), and the North American Meleagridae (turkeys, first occur in Miocene of North America); more primitive but related to all the above are the Cracidae-Megapodiidae (see above).

The family Phasianidae is first known in the

early Oligocene of North America and Europe (different subfamilies on each continent). In Europe it was taxonomically diverse in the mid to late Cenozoic and is most diverse in Asia and islands of the Southwest Pacific today. All of the genera of phasianids occurring at present in Australia belong to the Old World subfamily, Phasianinae. One endemic genus (*Anurophasis*) has diverged from the Old World forms, but *Coturnix*, *Synoicus*, and *Excalfactoria* also occur in the Old World and Southwest Pacific. Since the Australian diversity and endemism are so low, the Asian and Southwest Pacific diversity so high, coupled with the conspecificity of three of the four Australian genera with Old World forms, dispersal southwards along the Indomalaysian route is the most probable explanation for the pheasants and quail presently known in Australia.

Turnicidae. Bustard quail; Pleistocene-Recent; 2 genera (*Turnix*, *Ortyxelos*), only *Turnix* occurs in Australia; family restricted to Old World, Southwest Pacific, and Australia/New Guinea with a fossil record in Asia and Australia; most closely related family, the Australian endemic Pedionomidae, nearest relatives to birds outside of Turnicidae-Pedionomidae uncertain (see Bock and McEvey, 1969) but most likely lie within the Gruiformes.

Pedionomidae. Collared hemipode; no fossil record; 1 genus and species present in Australia; most closely related family, the Turnicidae.

The bustard quail (Turnicidae) are generically most diverse in Africa where both genera in this family occur. *Turnix* is the only genus that reaches Australia and is itself most diverse there and in the Southwest Pacific. With this evidence alone, the most likely path of interchange between Australia and the rest of the world is Indomalaysian. But in which direction did the movement occur? The Pedionomidae, endemic to Australia, may well be the most closely related, yet perhaps more primitive group (retains hallux; Bock and McEvey, 1969), to the Turnicidae. With lack of phylogenetic analyses that point to the group of birds most closely related to the Turnicidae-Pedionomidae, it is not possible to suggest

which dispersal route(s) may have been utilized by ancestral turnicids or pedionomids. Similarity between the Turnicidae of the Old World and Australia could be accounted for by a mid-late Tertiary interchange, either northwards or southwards, along the Indomalaysian route, and the differences in diversity between Australia and Africa are not great enough to significantly favour either possibility.

Gruidae. Cranes; Eocene-Recent; Miocene-Recent in Australia; family nearly cosmopolitan except for South America and New Zealand; 4 living, 8 extinct genera; 1 genus (*Grus*) in Australia; family most diverse and with greatest endemism in Africa; nearest relatives within the Gruiformes, possibly the Aramidae (limpkins) of the New World (first recorded in Oligocene of North America (R. Emry, S. Olson, pers. comm., 1972), the Psophiidae (trumpeters, presently restricted to South America, with no fossil record), or the Eogruidae (early Oligocene of Asia (see Cracraft, 1969)), Rallidae, Heliornithidae, Eurypygidae.

The family Gruidae had differentiated by the early-mid Eocene in Holarctica and apparently was present in Australia by the mid-Miocene (Stirton, Tedford, and Woodburne, 1968). In the Recent fauna, the Gruidae are most diverse in the Old World, with only the genus *Grus* extending into the New World and Australia. *Grus* is most varied in Asia, with only two of the total nine species in the genus occurring in Australia-New Guinea (including the endemic *G. rubicunda*). Thus, based on the low endemism and diversity of the Gruidae in Australia, the high diversity in the Old World, and lack of conflicting evidence from the fossil record, southward movement over the Indomalaysian route would best explain the present record of cranes in Australia.

Rallidae. Rails; Cretaceous or Eocene-Recent¹⁰; probably mid-Miocene-Recent in Australia; family cosmopolitan; 51-52 living, 27 extinct genera; 13-14 living genera in Australia; possibly one extinct fossil genus (Stirton, et al.,

¹⁰ If *Telmatornis* included in the Rallidae (fide Brodkorb (1967)), family first known in Cretaceous; Cracraft (1969) has presented convincing arguments for placing this genus in a separate family, and thus the first record of the Rallidae is Eocene.

1968) in the mid-Miocene of central Australia; greatest diversity in Southwest Pacific region with slightly less diversity in Old World and New World; greatest number of endemic genera in South America, but nearly as many in Southwest Pacific; closest relatives of Rallidae lie within the Gruiformes, perhaps the Gruidae, Aramidae, Psophiidae, Turnicidae, Heliornithidae, Eurypygidae (see above).

At least nine genera of rallids are present in the living avifauna of Australia, of which three are endemic to Australia and/or New Guinea: *Tribonyx* (= *Gallinula* in Condon, 1973; rarely a vagrant to New Zealand), *Rallicula*, and *Megacrex*. To this list can be added *Eula-beornis* and *Gymnocrex* that are endemic to Australia-New Guinea and some islands in the Southwest Pacific. All of these genera contain only one species in Australia, except *Rallicula* with four. Three other genera range through Australia-New Guinea-Southwest Pacific-Asia (*Rallina*, *Amaurornis*, *Poliolimnas*), while the remaining forms have cosmopolitan (*Rallus*, *Porzana*, *Gallinula*, *Fulica*) or nearly cosmopolitan (*Crex*, *Porphyrio*; not found in the New World) distributions. Although genera that occur in the living avifauna of Australia have very brief (Pliocene or younger) fossil records, other members of the family are known far back into the Tertiary.

If identifications are correct, well differentiated rails were present in Europe during the Eocene and Oligocene when Australia was still attached to Antarctica. This information, coupled with the low degree of endemism and lack of speciation of endemic forms in Australia, suggests that the Indomalaysian route or a transoceanic route utilized late in the Cenozoic was probably responsible for rails presently known in Australia. The great diversity and high endemism in the Southwest Pacific is probably due to geographic isolation imposed by the insular nature of the region as well as a long history in this area, most of which has been closely associated with Asia through the Cenozoic; the diversity in South America may be due to a combination of environmental diversity as well as a long history of the group there. Perhaps the rallids were one of the groups present in South America during the

early Tertiary (no fossil record corroborates this, however) that did not successfully cross the Antarctic sweepstakes route into Australia.

Otididae. Bustards; Eocene-Recent; late Pliocene-Recent in Australia; family restricted to Old World and Australia-New Guinea; 11 genera in recent avifauna, 1 extinct fossil genus; 1 living genus (*Eupodotis* = *Ardeotis*) in Australia; most closely related family probably the extinct Gryzaidae (early Pliocene of eastern Europe); other closely related forms probably within the Gruiformes, perhaps the Cariamidae (seriemas, Pleistocene-Recent, South America).

Bustards, restricted to the Old World and Australia and particularly diverse in Africa, are first recognized in the middle Eocene of Europe. Modern genera first appear in the Miocene (*Chlamydotis*) and Pleistocene (*Otis*, *Tetrax*). Only one species of one genus (*Eupodotis australis*) is known in Australia, and its entrance seems most probably to have been via southward expansion along the Indomalaysian route perhaps as early as mid-late Pliocene.

Jacaniidae. Jacanas; Miocene-Recent; no fossil record in Australia; family pantropical; 5 living, 1 extinct genera; 1 genus (*Jacana*) living in Australia at present; greatest diversity and endemism in Old World; closest relatives probably the Phegminornithidae (early Miocene, North America); other close relatives within the Charadriiformes (possibly the Rostratulidae (Jehl, 1968), first recognized in Eocene of Europe, at present cosmopolitan except North America or the Scolopacidae (see below)).

Only one genus (and one species) of Jacaniidae is present in Australia at present. Peters (1934) recognized an endemic genus, *Irediparra* (*I. gallinacea*), for the Australian-Southwest Pacific, but Slater (1971) included this form in *Jacana*, which otherwise has a range restricted to the New World (where it has a Pleistocene to Recent record).

Restudy of the Australian form is in order, however, to determine if it really is closer to the New World or Old World forms. It appears that the Indomalaysian route was employed (with southward movement) in the initial entrance of this family into Australia because of the low diversity in Australia and the greater

diversity in the Old World. Also the present restriction of the family to the warm, humid tropics argues against the previous use of a cool, temperate high latitude dispersal route.

Haematopodidae. (Haematopodinae in Scolopacidae of Brodkorb, 1967). Oyster-catchers; Miocene-Recent; no fossil record in Australia; family cosmopolitan; 1 genus; closest relatives probably one of the following: Palaeotringinae (Cretaceous-Eocene, North America and Europe), Scolopacidae (cosmopolitan at present; first occurs in Eocene of Europe), Aphrizidae (= Arenariidae; no fossil record, nearly cosmopolitan but not in Africa), Charadriidae (cosmopolitan, first occurs in early Oligocene of North America and Europe), Phalaropidae (Holarctic, no fossil record), Rostratulidae (see above), Burhinidae, and Recurvirostridae (see below).

The oyster-catchers are represented by two species in the only genus of the family, *Haematopus*, in the Australian avifauna. One species (*H. fuliginosus*) is endemic to Australia, while the other is nearly cosmopolitan. The group is first recognized in the early Miocene of North America. Certainly the Indomalaysian route accounts for the present cosmopolitan nature of *Haematopus*, but what the history of the family has been and where it originated are not clear. The appearance of the genus in North America in the Miocene could be owing to origin there or somewhere else, even Australia, and thus whether movement along the Indomalaysian route of *Haematopus* has been north or south, and which route was used by the ancestor of the oyster-catchers remains to be determined.

Charadriidae. (Charadriinae of Mayr and Amadon, 1951; Brodkorb, 1967). Plovers; Oligocene-Recent; no fossil record in Australia; family cosmopolitan; 31 living, 3 extinct genera; 5 living genera in Australia, most of which are winter residents only, with one endemic genus, *Peltohyas*; greatest diversity in Old World; greatest endemism in Old World but for a single continent in South America; nearest relatives as in Haematopodidae (see above), possibly closest to the Glareolidae (Jehl, 1968).

Four of the five genera of plovers and dotterels occurring in Australia are cosmopolitan in distribution (except *Vanellus*, which does

not occur in the New World), and all except *Vanellus* have only winter ranges in Australia. Only *Peltohyas*, with one species, is endemic to Australia. The high diversity and endemism of this group in the Old World in comparison to that of Australia suggest that the plovers most probably dispersed south along the Indomalaysian route or across oceanic barriers rather late in the Cenozoic. The Paleogene occurrence of the charadriids in Holarctica does not contradict this conclusion.

Arenariidae (often included in the Charadriidae or Scolopacidae). Turnstones; no fossil record; family cosmopolitan; 2 living genera; 1 genus (*Arenaria*) in Australia; most diverse and endemic in North America; nearest relatives possibly the Charadriidae or Phalaropodidae (Jehl, 1968) (see above).

Since the main centre of diversity (which is low) of this family is in North America and only one cosmopolitan species (*Arenaria interpres*) occurs in Australia, dispersal to Australia most likely occurred as a southward expansion of the group along the Indomalaysian route.

Scolopacidae. (Scolopacinae of Mayr and Amadon, 1951; Brodkorb, 1967). Snipe, sandpipers; Eocene-Recent; no fossil record in Australia; family cosmopolitan; 27 living, 3 extinct genera; 11 living genera in Australia; New and Old World with about equal diversity and endemism, including Australia and the Southwest Pacific; about one-third of genera in family cosmopolitan; closest relatives probably among the following: Palaeotringidae (see above), Rostratulidae (cosmopolitan except for North America, first known in Eocene of Europe); Charadriidae, Aphrizidae, Phalaropodidae, or Haematopodidae (see above); Jehl (1968) suggests the Gallinagoninae and Calidrinae.

The Scolopacidae are first known in the Eocene of Europe. Of those genera in Australia at present, *Limosa* is first known from the Eocene¹¹ of Europe, *Numenius* from the mid-Miocene of Europe, *Bartramia* from the mid-Pliocene of North America, *Calidris* from the early Pliocene of North America, *Philomachus* from the early Pleistocene of Asia.

¹¹ All of the early Tertiary forms need re-evaluation to establish the presence of living genera during the Paleogene.

All of the genera occurring in Australia are only boreal winter visitors, most not breeding in Australia, except for *Scolopax*. Six of the eleven genera have cosmopolitan (or nearly so) distributions, two are primarily New World genera that occasionally wander to Australia, three are restricted to Australasia and the Old World.

Quite clearly the Indomalaysian route is in use at present, with many genera following this route south during the boreal winter. Some forms (*Tryngites*, *Bartramia*), however, occasionally visit Australia using neither the Antarctic nor the Indomalaysian route but cross broad oceanic barriers. What the history of the wide ranging Scolopacidae has been is uncertain, as is its place of origin. What can be deduced from the above data is that many of the genera presently in Australia have probably made use of, and are still using, the Indomalaysian route.

Recurvirostridae. (Recurvirostrinae of Mayr and Amadon, 1951). Avocets and stilts; Eocene-Recent; no fossil record in Australia; family cosmopolitan; 3 living, 2 extinct genera; all living genera occur in Australia; most diverse in Australia; one genus to Australia (*Cladorhynchus*); most closely related family probably one of the following: Phalaropodidae (see below), Jacanidae, Haematopodidae (Jehl, 1968), Charadriidae, Aphrízidae, Scolopacidae, Rostratulidae, or Palaeotringidae (see above).

Australia is the only continent that supports all three genera (*Himantopus*, *Cladorhynchus*, *Recurvirostra*) of avocets and stilts; *Cladorhynchus* is restricted to Australia. *Himantopus* contains only one species (and that is cosmopolitan), while *Recurvirostra* contains four that are each restricted in range, one being endemic to Australia. With the fossil record of the group being as old as it is (if *Presbyornis* and *Coltonia* are accepted as members of the family (Brodkorb, 1967)), its history begins at least by the early Eocene). Combined with the above data on endemism and diversity of the group, an Antarctic route cannot be discounted for initial entrance into Australia. Similarly, a southwards dispersal along the Indomalaysian route cannot be discounted. The present cosmopolitan distribution undoubtedly is due to late

Cenozoic movement (north or south) along the Indomalaysian route or oceanic dispersal.

Phalaropodidae. (Phalaropinae of Mayr and Amadon, 1951; Brodkorb, 1967). Phalaropes; no fossil record; family cosmopolitan with breeding ranges exclusively in Holarctica, boreal winter ranges in southern hemisphere; 1 living genus; closest relatives probably one of following: Palaeotringidae, Rostratulidae, Scolopacidae, Charadriidae, Haematopodidae (see above); Jehl (1968) suggests the Tringini and Prosobonini.

Phalaropus includes three species, two of which have nearly cosmopolitan ranges and a third that breeds in the New World, spending its non-breeding season in Australia. Because the family is represented by a single genus that is neither very diverse nor endemic anywhere in the world, dispersal has probably been rather recent. In the case of *P. tricolor* that breeds in North America, neither Antarctic nor Indomalaysian routes have been utilized, but in the case of the other two species, movement along the Indomalaysian route seems the most probable explanation for present distributions. Determination of direction of movement is more difficult. Because Australia is used only as a boreal winter refuge by birds in this family, some workers have suggested that the group has originated elsewhere and expanded into Australia. Darlington (1957), however, rightly has raised objection to such interpretations (see above).

Burhinidae. Thicknees, stone curlews; Miocene-Recent; family cosmopolitan; 1-2 living genera (including *Orthorhamphus* in *Esacus*; some (Condon, 1973) consider only one genus, *Burhinus*, present) which occurs in Australia; one extinct genus (*Milnea*) from the Miocene of Europe; greatest endemism and diversity in Asia and Australia; closest relatives perhaps Jacanidae, Haematopodidae (see above; also Jehl (1968)), Glareolidae (see below), Dromadidae (coast and islands of north and west side some other family within the Charadriiformes. of Indian Ocean, no fossil record) or perhaps

The burhinids are most endemic and diverse in the Old World and Australia (*Esacus*, *Burhinus*), with only one genus (*Burhinus*) extending into the New World. Some workers

(Peters, 1934) have suggested that a third genus (*Orthorhamphus*), endemic to Australia, should be recognized. The family is not a relatively recent derivation but has a history extending at least into the early Miocene of Europe and mid-Miocene of Australia. Similarity of forms between the Old World and Australia are most probably due to dispersal across the Indomalaysian route, but what the direction of movement (north or south) has been is ambiguous. If the movement has been north, which dispersal route was employed by burhinid ancestors?

Glareolidae. Pratincoles or swallow plovers, courses; no fossil record; family restricted to the Old World-Australia-New Guinea-Southwest Pacific; 5 living genera; 2 living genera in Australia (both in the subfamily Glareolinae, the pratincoles); most diverse in Africa; one endemic genus each in Africa and Australia while remaining genera range over Old World or Old World-Australasia (excluding N.Z.); nearest relatives probably among the following: Charadriidae (Jehl, 1968), Burhinidae, Dromadidae (see above), Thinocoridae (temperate South America, no fossil record), Chionididae (southern South America and Antarctic Islands, possibly Pleistocene record in southeastern Australia, J. van Tets, pers. comm., 1972), Rostratulidae, Haematopodidae, Scolopacidae, Recurvirostridae, Phalaropidae (see above and below).

The pratincoles are represented by two genera in Australia, one endemic (*Stiltia*) and another that is widely distributed throughout the Old World (*Glareola*), though most diverse in Africa. The one species of *Glareola* (*G. maldivarum*) that occurs in Australia is only a non-breeding visitor. Closely related to the pratincoles are the Cursoriinae, considered by most workers to be the more primitive subfamily in the Glareolidae, that are entirely restricted to the Old World and particularly diverse in Africa. The family as a whole is decidedly more diverse and endemic in the Old World than in Australia, and this accompanied by the phyletic conclusions favours dispersal of the glareolids southward along the Indomalaysian route.

Laridae. (Sterninae and Larinae of Mayr and Amadon, 1951; Brodkorb, 1967). Gulls and

terns; Oligocene¹²-Recent; probably Miocene-Recent in Australia; family cosmopolitan; 15 living, 6 extinct genera; 8 living genera in Australia; possibly 1 extinct endemic genus in Australia, described by DeVis (1905); highest diversity in New World, although not decidedly greater than in Old World; half of genera of Larinae cosmopolitan, 2 endemic to Holarctica, 1 to Galapagos; more than half of genera of Sterninae cosmopolitan, 2 endemic to South America, 2 to Australia and/or New Guinea and Southwest Pacific; nearest relatives probably Stercorariidae (skuas, oceanic birds breeding in Arctic and Antarctic, wintering on all oceans, known as fossils only from Pleistocene of North America) (Hudson *et al.*, 1969); the highly specialized Rhynchopidae (skimmers, North America, South America, Africa, and Asia, no fossil record), or perhaps birds within Brodkorb's Scolopacidae (Palaeotringinae, Rostratulinae, Scolopacinae, Aphrizinae, Charadriinae, Phalaropodinae, Haematopodinae), Recurvirostridae, Jacanidae, Burhinidae, Dromadidae, Glareolidae, Thinocoridae, Chionididae, or any other members of the Charadriiformes.

The terns are more diverse generically in Australia (as well as the rest of the world) than are the gulls. Only one genus of larine, *Larus*, with three species, is known in Australia, a very low diversity when compared with that of the group elsewhere in the world. In contrast, terns (Sterninae) are quite diverse, with seven of the nine genera in the subfamily represented in the Australian avifauna. Five of the seven genera are nearly, if not completely, cosmopolitan. The remaining two (*Procelsterna*, *Gygis*) are endemic to Australia and/or New Guinea and some of the Southwest Pacific islands.

Gulls are first recognized in the mid-Oligocene of Europe, and *Larus* had differentiated by the early Miocene in Europe and North America. Since the subfamily is so little differentiated and not diverse in Australia even today but is diverse outside of Australia, present members of this group most probably arrived in Australia via southward dispersal along the Indomalaysian route relatively recently. The

¹² *Halcyornis*, from the Eocene London Clay fauna; once thought to be the oldest Laridae, has recently been transferred to the Coraciiformes (Harrison and Walker, 1972).

subfamily's occurrence in the Paleogene of Europe does not argue against this conclusion.

The Sterninae are first known in Miocene sediments of Europe and occur in the mid-Miocene of Australia (Stirton, Tedford, and Woodburne, 1968). They are most diverse in Australia and the Southwest Pacific today, but most genera are cosmopolitan. Based on the subfamily's endemism, diversity, and distribution no clear decision concerning their area of origin can be made.

Thus, at present, southward movement along the Indomalaysian route most probably accounts for the presence of the known *Larinae*, but area of origin and route employed by the Sterninae is uncertain. The most recent episode of dispersal of the terns has undoubtedly been Indomalaysian or oceanic, but in what direction (north or south) and what route was utilized by the ancestors of the terns, Antarctic, Indo-malaysian, or oceanic?

Rostratulidae. (Rostratulinae of Mayr and Amadon, 1951; Brodkorb, 1967). Painted snipe; Eocene-Recent; no fossil record in Australia; family cosmopolitan except for New Zealand and North America; 2 living, 1 extinct genera; only 1 genus (*Rostratula*) in Australia; one genus endemic to South America, the other to the Old World and Australia; nearest relatives probably one of the following: Palaeotringidae, Scolopacidae, Aphrizzidae, Charadriidae, Phalaropodidae, Haematopodidae, or Jacanidae (see above).

At present a single species of painted snipe, *Rostratula bengalensis*, occurs in most of the Old World (excluding Europe) as well as in Australia and New Zealand. Although it has probably recently dispersed across the Indo-malaysian route, the direction of dispersal of this family or of its ancestors is not obvious. The only other living rostratulid is the South American *Nycticryphes*. The Recent disjunct distribution of the family suggests that previously it may have been much more widespread, or that by chance one population accidentally established itself in either South America or the Old World, while the main population remained in the homeland that spawned the founder. Because phyletic relationships have not been adequately determined for

the group, it is impossible to determine which case is more probable. In addition to the living forms, an extinct genus has been reported from the middle Eocene of Germany (which needs re-examination to ascertain its identity). If correctly identified, it has significance in signaling the differentiation of the family at an early date, for nothing is known of the group's world-wide distribution at that time. Thus, distributional history of the rostratulids is undecipherable at present; although the Indo-malaysian route has probably been used most recently, direction of that dispersal is quite uncertain.

Columbidae. Doves and pigeons; Miocene-Recent; Pleistocene-Recent in Australia; family cosmopolitan; 58 living, 3 extinct genera; 15-27 living and 1 extinct genera in Australia-New Guinea (15 living genera endemic to Aust.-N.G.-SW Pacific plus possibly endemic fossil genus described by DeVis that needs re-evaluation); most diverse and endemic in Australia and the Southwest Pacific; nearest relatives the extinct dodos and solitaires (Raphidae) of the Mascarene Islands in the Indian Ocean and possibly the sand grouse (Pteroclididae) at present occurring in much of the Old World (first recognized in the late Eocene-early Oligocene of Europe; Storer (1971) following Maclean (1967) has placed the sand grouse in the Charadriiformes; Sibley (1966), suggests relationship to both groups); relationships of the Columbiformes uncertain, perhaps showing closest affinity with the Psittacidae, more distant to the Charadriiformes or Galliformes.

At present the pigeons form a group that is extremely diverse and highly endemic in the Southwest Pacific and Australia, and only moderately so in South America, Asia, and Africa. All four subfamilies (Treroninae, Columbinae, Gourinae, Didunculinae or Ptilinopinae, Columbinae, Macropygiinae, Turturinae of Condon (1973) are represented in the Southwest Pacific and/or Australia, but only two (Treroninae, Columbinae) are represented elsewhere. The fossil record of the group is so incomplete as to be useless (except that it indicates the group had differentiated at least by the Miocene and occurred in Holarctica at that time), as is the understanding of what avian group is most closely related to the

pigeons. However, due to such great diversity and endemism at both the generic and the specific levels in Australia when compared to the pigeon faunas of the rest of the world, an origin of the group and/or a long history on that southern continent should not be discounted, nor should the possibility of an Antarctic dispersal of the group originally.

Recent movement along the Indomalaysian route accounts for generic similarity between Old World and Australian forms, but such similarity in no way demands a northern origin for the group—it demands only interchange between the two land masses. There may, in fact, have been movement both north and south along this route when individual genera are considered.

Psittacidae. Parrots; Miocene-Recent; Pleistocene-Recent in Australia; family with pan-tropical distribution at present, Tertiary representatives in Europe; 81 living, 4 extinct genera; 37 living genera in Australia of which 37 are endemic to Australia-New Guinea-Southwest Pacific; subfamilies Loriinae, Cacatuinae, Micropsittinae endemic to Australia-New Guinea-Southwest Pacific; besides 2 endemic subfamilies in New Zealand, only subfamily occurring outside of Australia (also occurs in Australia) is the Psittacinae; Condon (1973) has recently proposed the designations Cactuidae (Proboscigerinae, Calyptorhynchinae, Cacatuinae), Psittacidae (Palaeornithinae), Loriidae, Apopsittidae, Polytelidae, Platycercidae (Pezoporinae, Lathaminae, Platycercinae) for Australian parrots; greatest diversity and endemism in Australia-New Guinea-Southwest Pacific while South America has moderate diversity; nearest relatives are uncertain but may be among the Columbiformes (pigeons, sand grouse) or the Cuculiformes (turacos, cuckoos, and allies).

Although the relationships of this group to others is not sufficiently well understood, the great diversity and endemism of the group in Australia, New Guinea, and the Southwest Pacific, in comparison to the strikingly low diversity of that group in Asia and Africa (with only two and four genera respectively), does not *obviously* suggest a northern origin for the group. Instead, I believe, it strongly suggests that more serious consideration should

be given the possibility of an origin and/or early radiation on the southern continents and an Antarctic dispersal of the group or perhaps even an origin within Australia. Undoubtedly the Indomalaysian route has most recently been used in assuring similarity of the African and Asian forms with those of the Southwest Pacific and Australia.

Cuculidae. Cuckoos; Eocene-Recent; no fossil record in Australia; family cosmopolitan, 37 living and 2 extinct fossil genera; 9-10 living genera in Australia; one (*Microdynamis*) of which is endemic and 3 of which are endemic to Australia - New Guinea - Southwest Pacific (*Scythrops*, *Rhamphomantis*, *Caliechthrus*); greatest diversity of family in Southwest Pacific and Asia with twice as many endemic genera in the New World as the Old; most closely related family probably the turacos (*Musophagidae*) now restricted to Africa but with a Tertiary record (Eocene-Miocene) in Europe.

Cuculids are represented by 9-10 living general in Australia, only one of which is endemic. This is in marked contrast to the great diversity and high endemism of the family in the Southwest Pacific and Asia. As the nearest relatives of the cuculids are probably the musophagids (turacos), living in Africa today (and had a history in early to mid-Tertiary Europe), this group probably dispersed into Australia southwards along the Indomalaysian route. Endemism among the cuculids is highest in the New World and the group had differentiated there by the mid-Eocene; so, an Antarctic dispersal route cannot be completely ruled out but seems less likely based on known evidence owing to the group's low endemism in Australia. Because faunal interchange between North America and Europe was high as late as the early Eocene (McKenna, 1972a), cuculids might well be expected in Europe if present in North America; thus histories in both the Old and the New World have probably been long, and could account for such great diversity and endemism in these areas. Cuculids may be one group, that although present in South America at a time when the Antarctic dispersal route was open, did not have the right sweepstakes ticket!

Marchant's (1972) suggestion that the

genera *Cacomantis* and *Chrysococcyx* were derived from a common ancestor in Antarctica and then spread north into Australia and Africa respectively, does not take into account the probable pre-early Cretaceous (ca. 200 m.y. B.P.) or early Cretaceous separation of Africa and East Antarctica (see figs. 1-2) and in no way invalidates the above discussion. This timing of the Afro-Antarctic break-up is probably too far in the past to have permitted dispersal between Australia and Africa of the modern avian families, let alone closely related genera. Certainly the warm tropical vegetational belt that lined much of southern Asia and the Mediterranean area during the early and into the mid-Tertiary would have provided an excellent corridor for distribution between Australia and Africa, once Australia had moved far enough north to allow such exchange to take place (by the Miocene). Isolation imposed when such a corridor was gradually destroyed during the Neogene by increasingly cooler world-wide climate, could easily explain the *Cacomantis-Chrysococcyx* distribution seen today.

Strigidae. (Striginae of Mayr and Amadon, 1951). Owls; Eocene-Recent; no fossil record in Australia; family cosmopolitan, 28 living and 3 extinct fossil genera; 2 genera in Australia; many genera cosmopolitan with endemism nearly the same in both New and Old Worlds; group most diverse in South America, Southwest Pacific, and Asia; nearest relatives probably the Tytonidae (barn owls; Ford, 1967 *et al.*) also cosmopolitan in distribution (known as fossils from the Miocene of Europe, elsewhere only Pleistocene or later), and the Protostrigidae (Eocene, North America) and more distantly the Caprimulgiformes (see below), and perhaps the Falconiformes.

Only two genera of typical owls occur in the living Australian avifauna, while the group is quite diverse elsewhere, particularly in the Southwest Pacific, Asia, and the New World. Apparently *Ninox* (with four Australian-New Guinean species) and *Uroglaux* (1 species in New Guinea; genus restricted to New Guinea and the Southwest Pacific) or forms that gave rise to them, dispersed southwards from Asia and the Pacific Islands to Australia along

the Indomalaysian route. Otherwise, greater endemism and diversity would certainly be expected on a continent with such a small number of nocturnal avian carnivores.

Tytonidae (including the Phodilidae, which Brodkorb (1971a) isolates as a separate family; Tytoninae of Mayr and Amadon, 1951). Barn owls; Miocene-Recent; Pleistocene-Recent in Australia; family cosmopolitan; 2 living genera; 1 genus (*Tyto*) in Australia; *Tyto* cosmopolitan, but other genus, *Phodilus*, endemic to Asia and the Southwest Pacific; greatest diversity and endemism of family in Asia and the Southwest Pacific; closest relatives probably the Strigidae or the Protostrigidae (see above).

Because the greatest diversity (both generic and specific) of this group occurs in the Old World and Southwest Pacific (only *Tyto* reaches Australia and *Tyto alba* reaches the New World), southward movement through Indomalaysia seems the most likely route between Australia and the rest of the world. *Phodilus* in addition to *Tyto* occurs in the Old World; another extinct genus in the subfamily Phodilinae occurred in the Miocene of Europe.

Podargidae. Frogmouths; no fossil record; restricted to Asia-Southwest Pacific-Australia-New Guinea; 2 living genera, *Podargus* (Aust.-N.G.-SW Pac.) and *Batrachostomus* (As.-SW Pac.); nearest relatives within the Caprimulgiformes including Caprimulgidae, Aegothelidae (see below), Aegialornithidae (Eocene-Oligocene of Europe), Nyctibiidae (restricted to American tropics with a Pleistocene record in South America), or the Steatornithidae (restricted to northern South America, no fossil record).

Aegothelidae. Owlet frogmouths; Pleistocene-Recent; Miocene-Recent in Australia; at least 1 genus (*Aegotheles*); presently restricted to the Southwest Pacific-New Guinea-Australia but has Pleistocene record in New Zealand; most diverse specifically in New Guinea; nearest relatives in the Caprimulgiformes (see above, including Podargidae).

Caprimulgidae. Nightjars; Pleistocene-Recent; no fossil record in Australia; family cosmopolitan; 19 living genera; 2 genera (*Eurostopodus* and *Caprimulgus*; Condon (1973) recognized only the latter) in Australia-New Guinea; greatest diversity in the New World, particularly in South America; largest numbers of

endemics in the New World, particularly in South America; closest relatives within the Caprimulgiformes (see above).

The Caprimulgiformes, including the three previously mentioned families (Podargidae, Aegothelidae, and Caprimulgidae), are first represented in the Eocene/Oligocene of Europe by the Aegialornithidae. An aegothelid has been recovered from Miocene sediments in Australia, but the only other record of the order is in the Pleistocene from several different localities in many parts of the world. The order is composed of two families (Podargidae, Aegothelidae) endemic to Australia-New Guinea-Southwest Pacific (and Asia in the case of the Podargidae), two endemic to tropical South America (Nyctibiidae, Steatornithidae), and one with a cosmopolitan distribution (Caprimulgidae).

In the case of the cosmopolitan Caprimulgidae, entrance into Australia appears to have been via southward movement along the Indomalaysian route. Only two genera, one cosmopolitan (*Caprimulgus*) and another shared with the Old World (*Eurostopodus*), occur in Australia. The family is much more diverse with more endemic species in the Old World than in Australia, but most diverse and endemic in the New World. Such data would seem best explained by a southward dispersal along the Indomalaysian route.

Dispersal routes utilized by the other two families or their ancestors are uncertain, however. They are either entirely (Aegothelidae), or nearly (Podargidae), restricted to and most diverse in Australia-New Guinea-Southwest Pacific including New Zealand. Only the Podargidae range into Asia. What relationships they have to the Caprimulgidae and the American tropical forms (Nyctibiidae, Steatornithidae) are uncertain, and so too is the route into Australia used by both groups or their ancestors. Did they develop in Australia and/or the Southwest Pacific and spread north along the Indomalaysian route? If so, did the ancestral stock arrive originally via the Antarctic or the Indomalaysian route? Although caprimulgiforms are known only from the Eocene/Oligocene of Europe, because of generally poor records in the rest of the world at this time,

it is impossible to determine their geographic range; primitive caprimulgiforms might well have been more widespread, and if such were the case, the Antarctic route should not be dismissed.

Hemiprocnidae. Crested swifts; Pleistocene-Recent; no fossil record in Australia; 1 genus; family restricted to New Guinea-Southwest Pacific-Asia; most diverse and endemic in the Southwest Pacific; closest relatives probably the swifts (Apodidae; but Sibley, 1960, thought this due to convergence but later (Sibley and Ahlquist, 1972) noted close similarity) that have a cosmopolitan distribution (see below).

The crested swifts form a small group (one genus with three species) that is most diverse in the Southwest Pacific. It is probably most closely related to the swifts (Apodidae) that occur throughout the world. Where the group originated is uncertain, but its dispersal between Australia and the rest of the world seems intimately tied with the Indomalaysian region. At present either a northward or southward dispersal could have occurred, depending on area of origin.

Apodidae. Swifts; Eocene or Oligocene-Recent; no fossil record in Australia; family cosmopolitan; 16 living, 1 extinct genera; 3-5 living genera in Australia; diversity is low in Europe and New Zealand but about the same for all other continents; closest relatives, the Hemiprocnidae (see above), perhaps the Trochilidae (hummingbirds, with a New World, primarily South American, distribution and a Pleistocene record there; Sibley, 1960; Cohn, 1966, however, has suggested the two groups convergent); and perhaps more distantly the Caprimulgiformes (see above).

All of the genera of swifts that occur in Australia-New Guinea are monotypic or contain only a few species (*Hirundapus*, *Apus*, *Collocalia*, *Chaetura*, *Mearnsia*); only the first three are recognized by Condon (1973) and are more diverse in the Southwest Pacific and the Old World. No endemic genera occur in Australia. The fossil record indicates that the family was present in the Old World by the Eocene or Oligocene, and both *Apus* and *Collocalia* differentiated there by early Miocene. The recent distributional and diversity data

suggest that southward movement over the Indomalaysian route into Australia is most probable.

Alcedinidae. (Halcyonidae of Brodkorb, 1971a). Kingfishers; Eocene/Oligocene-Recent; no fossil record in Australia; family cosmopolitan; 14 living, 1 extinct genera; 7 living genera in the Australian-New Guinean region, one of which is endemic to New Guinea (*Clytoceyx*) and 3 of which are endemic to Australia-New Guinea-Southwest Pacific (*Melidora*, *Dacelo*, *Tanysiptera*); greatest diversity in Australia-New Guinea-Southwest Pacific region; similar endemism in Australia-Southwest Pacific and Old World regions; nearest relatives among the following: Todidae (todies of the Greater Antilles, Pleistocene record there), Motmotidae (motmots, restricted to the American tropics with a Pleistocene record there), and Meropidae (see below).

The kingfishers, first known in the Eocene or early Oligocene of Europe and later there in the Miocene, probably dispersed along the Indomalaysian route. Diversity of the group in the New World is so low (two genera in a single subfamily Cerylinae) as to suggest a rather recent arrival there, which thus argues against an Antarctic dispersal unless diversity in the past is revealed in the fossil record of the group when better known.

Meropidae. Bee eaters; Pleistocene-Recent; no fossil record in Australia; distributed over much of Old World, Southwest Pacific-Australia; 7 living genera; 1 genus (*Merops*) in Australia; greatest diversity and endemism in Africa; closest relatives among the Alcedinidae, Todidae, Motmotidae (see above), and Upupidae (hoopoes, restricted to warm parts of Old World, Pleistocene record in Old World) and Coraciidae and Bucerotidae (restricted to Old World and Australasia, with greatest diversity in Old World and Eocene-Oligocene record in Europe).

Coraciidae. Rollers; Eocene/Oligocene-Recent; no fossil record in Australia; family restricted to Old World and Australia-New Guinea-New Zealand; 5 living, 1 extinct genera; 1 genus (*Eurystomus*) in Australia; greatest diversity and endemism in Africa (including Madagascar); nearest relatives probably Bucerotidae (see below), Upupidae, Alcedinidae, Motmotidae, Todidae, or Meropidae (see above).

Bucerotidae. Hornbills; Eocene-Recent; no fossil record in Australia; family occurs in Old World-Southwest Pacific-New Guinea; 12 living, 3 extinct genera; 1 living genus (*Aceros*), reaches New Guinea, greatest endemism in Southwest Pacific; nearest relatives probably among the following: Coraciidae, Upupidae, Alcedinidae, Motmotidae, Todidae, or Meropidae (see above).

The three families mentioned above (the bee eaters, rollers, and hornbills) have in common a great diversity only in the Old World, in contrast to a single genus representation in Australia and/or New Guinea. In addition the coraciids and bucerotids have a long history (Eocene/Oligocene-Recent) in the Old World. Thus, it seems most likely that southward movement along the Indomalaysian route accounts for their presence in the Australia-New Guinea avifauna.

In summary, there are several avian families (or their ancestors) in the Australian-New Guinean fauna whose initial dispersal to or away from that continent may well have been via either an Antarctic or an Indomalaysian sweepstakes route, or in some cases via oceanic dispersal. These families include (see Table 4):

- Casuariidae
- Dromornithidae
- Phalacrocoracidae
- Phoenicopteridae
- Anatidae (in part: Anseranatidae, Cereopini, Dendrocygnini, Oxyurini)
- Accipitridae (in part: Milvinae, Perninae)
- Megapodiidae
- Pedionomidae
- Turnicidae
- Haematopodidae
- Recurvirostridae
- Burhinidae
- Laridae (in part: Sterninae)
- Rostratulidae
- Columbidae
- Psittacidae
- Podargidae
- Agothelidae.

The remaining families not listed above have most probably moved south into Australia across the Indomalaysian route.

TABLE 4

Compilation of dispersal routes probably used between Australia and the remaining world by those non-passeriform families comprising the Australian avifauna.

INDOMALAYSIAN ROUTE (southward movement): Podicipedidae, Anhingidae, Ardeidae, Ciconiidae, Threskiornithidae, Anatidae (in part: Cygnini, Tadornini, Anatini, Aythiini), Accipitridae (in part: Elaninae, Circinae, Accipitrinae), Pandionidae (?N., ?S.), Falconidae, Phasianidae, Gruidae, Rallidae, Otidae, Jacanidae, Charadriidae, Arenariidae, Phalaropodidae, Scolopacidae, Glareolidae, Laridae (in part: Larinae), Cuculidae, Strigidae, Tytonidae, Caprimulgidae, Hemiprocnidae (?N., ?S.), Apodidae, Alcedinidae, Meropidae, Coraciidae, Bucerotidae.

ROUTE UNCERTAIN (Antarctic, Indomalaysian, and in some cases Oceanic dispersal possible): Casuariidae, Dromornithidae, Phalacrocoracidae, Pelecanidae, Phoenicopteridae, Anatidae (in part: Anseranatidae, Cereopsini, Dendrocygnini, Oxyurini), Accipitridae (in part: Milvinae, Perninae), Megapodiidae, Pedionomidae, Turnicidae, Haematopodidae, Recurvirostridae, Burhinidae, Laridae (in part: Sterninae), Rostratulidae, Columbidae, Psittacidae, Podargidae, Aegothelidae.

For many non-passeriform families (19 of the 46 families, five of these only in part) of the obligate terrestrial birds in the living, as well as the Tertiary avifauna of Australia, at least two hypotheses are available regarding route of original entrance. In many cases there is not enough information to permit a choice of one route in preference to another, and a most important point is that such a choice *cannot* be made at present, but does exist. Many of the non-passeriform families have utilized the Indomalaysian route most recently (Miocene and more recently). The mixing of the Australian and Old World avifaunas much more thoroughly than the mammalian faunas of these two areas has increased the difficulty of distinguishing Australian and Asian elements. This late Cenozoic utilization of the Indomalaysian route should not, however, be used to suggest a northern origin for all or most of the Australian non-passeriform avifauna. The striking similarity of the Australian-New Guinean fauna to that of Asia and the Southwest Pacific tells only of the latest episode in

a much longer interchange of birds between Australia and the rest of the world.

Discussion and Conclusions

Since Mayr's (1944a) classic paper suggesting that the major part of the Australian non-marine avifauna had been derived from the north, ideas concerning continental stability have radically changed. In the 1940's and as late as the 1950's, prevailing opinion among geologists, as well as biogeographers, demanded that continents had maintained their present positions with respect to one another throughout the Phanerozoic. Only with the pioneering work of Vine and Matthews (1963) on ocean floor magnetism did consensus begin shifting in favour of the currently popular theories encompassing continental drift, ocean floor spreading, and plate tectonics. Seen in the light of new and convincing evidence, Australia (including New Guinea) is no longer thought to have remained forever bounded by 45° South latitude and the equator, but instead is viewed as a truly incredible Tertiary voyager (a Noah's Ark, McKenna, 1973), moving north from a connection with the Antarctic some 50-55 m.y. ago to its present position, a journey of some 30-50 degrees of latitude. During its northward trek, profound changes in climatic regimes affecting Australia brought about the switch from a once cool, temperate vegetation covering much of the continent to the present varied and more zoned flora with the restricted cool temperate assemblages in the south, the tropical vegetation in the north (probably a Miocene innovation), and the widespread arid assemblages that characterize much of Australia today. Undoubtedly synchronous changes occurred in those faunas inhabiting the island continent, including the birds. Unfortunately, only the closing phases of Australia's avifaunal history are known, and thus such change cannot presently be documented for birds as it has been for the floras. What the late Mesozoic and early Tertiary terrestrial faunas were like is yet a mystery.

From a review (see first section of paper) of late Mesozoic and Cenozoic geologic history of Australia, other southern continents, and the ocean basins now separating them, it is

apparent that during the last 80 to 90 million years, two possible land routes (both probably sweepstakes routes in Simpson's (1940, 1953) and McKenna's (1972a-b, 1973) terminology) between Australia and the rest of the world have been available to terrestrial vertebrates: the Antarctic and the Indomalaysian. The Antarctic route was the only path not requiring dispersal across broad ocean basins that lay between Australia and the rest of the world from the late Mesozoic until the Eocene. Between that time and sometime during the Miocene, broad water barriers on the north and an increasingly hostile climate accompanied by an ever widening water barrier on the south essentially isolated Australia from the world's remaining land masses. During this period of profound isolation (that lasted perhaps as long as 20-30 million years), the avifauna, as well as the rest of the non-marine fauna, developed without much interference from the outside, only plagued, or advantaged, by the profound climatic changes that occurred as Australia drifted northward. In the mid to late Tertiary, as Australia neared its present position, the Indomalaysian route became the only major dispersal route that could be utilized by non-marine vertebrates. The Antarctic route was inactivated by the ever increasing breadth of the water barrier and the expansion of glaciation to a present continent-wide scale.

Paleoclimatological evidence suggests that the two dispersal routes had decidedly different climates throughout their entire existence. During the late Mesozoic and early Tertiary the Antarctic route was covered in many places with sizeable forests composed of *Nothofagus*, *Araucaria*, other primitive angiosperms, gymnosperms, ferns, and scouring rushes, among others, that is, a cool temperate flora much like that covering Australia during the early Tertiary. The climate was never tropical but was in no way the severe one affecting Antarctica today. The Indomalaysian route, on the other hand, has apparently supported a tropical vegetation throughout the Cenozoic, and seemingly its climate has remained much as it is today during the entire time it has served as a major route between Australia and the rest of the world.

If the modern families of birds, like the majority of modern placental mammalian families, had first developed and radiated mainly during the late Paleogene or Neogene in Holarctica, probably no choice of routes between Australia and the rest of the world used by different groups of birds would be necessary; the Indomalaysian route would be the only major stepping stone to Australia as suggested by Mayr (1944a) for the birds and by Matthew (1915) for vertebrate faunas, primarily mammals. Unlike modern placental mammalian families, however, a large number of the living avian families apparently differentiated during the Paleogene (see figure 10). Twenty of the forty-six avian families that make up the Cenozoic avifauna of Australia, had developed by the Eocene, some possibly as early as the Paleocene (Phalacrocoracidae), a few more by the Oligocene (Phasianidae, Charadriidae, Laridae), and most of the remaining families at least by the Miocene (excepting Megapodiidae, Turnicidae, Pedionomidae, Arenariidae, Phalaropodidae, Glareolidae, Podargidae, Aegothelidae, Caprimulgidae, Hemiprocidae, and Meropidae that have only a Pleistocene or Recent record). Differentiation undoubtedly occurred sometime before the groups first appeared in the fossil record, and thus probably more than just the twenty families with lengthy records also had records extending well back into the Paleogene. So, when considering the origin of the Australian avifauna, both Indomalaysia and Antarctica should be considered as possible routes of dispersal (see figure 9).

In summary, then, because of the early differentiation of modern bird families and the availability of two dispersal routes to and from Australia, one cannot assume that most, if not all, of the Australian non-marine avifauna originated in the north. Most probable route of initial entrance of ancestors of the following families or the families themselves is impossible to determine at present: Casuariidae (including *Dromaius* and *Casuarius*), Dromornithidae, Phalacrocoracidae, Pelecanidae, Phoenicopteridae, Anatidae (in part: Anseranatidae, Cereopsini, Dendrocygnini, Oxyurini), Accipitridae (in part: Milvinae, Perninae), Megapodiidae,

Pedionomidae, Turnicidae, Haematopodidae, Scolopacidae (in part), Recurvirostridae, Burhinidae, Laridae (in part: Sterninae), Rostratulidae, Columbidae, Psittacidae, Podargidae, and Aegothelidae. Determination of the most probable route of initial dispersal for such groups will have to await further studies on avian phylogeny and a more complete fossil record from the Australian late Mesozoic and Paleogene. A point to be stressed here, however, is that such Australian birds should be recognized as *groups of uncertain origin* and should not be lumped with those forms that most probably entered Australia from *either the north or the south*. At the species level approximately 43% (as well as 19 of the 46 families present in Cenozoic of Australia) of the non-passeriform, non-marine living avifauna of Australia fall in the category 'groups of unknown origin', hardly a small segment of the Australian bird fauna! The remaining groups, on the other hand, most probably arrived via the Indomalaysian dispersal route or in a few cases as long distance travellers across the Pacific or Indian oceans (Charadriiformes in particular).

Certainly arguments using the close similarity of the Southeast Asian and Australian avifaunas as an indicator that only the Indomalaysian route has served birds dispersing between Australia and the remaining world must be questioned. Such a similarity reflects the recent, close apposition of the Palearctic and Australian continental masses and is certainly indicative of interchange, but movement of faunas could have been northward as well as southward. Such close similarity does *not* rule out the possibility of an Antarctic dispersal at some time in the past. Such southern dispersal would have occurred at a time much more distant in the past than that across Indomalaysia. The fauna that arrived in Australia via an Antarctic route would certainly have evolved during the 40 million years since their arrival there, especially as they were probably in extreme isolation for 20 million years. Owing to the climatic changes taking place as Australia drifted northward, undoubtedly there were concomitant changes, perhaps even large-scale extinctions, in the faunas that had reached Australia across

Antarctica.¹³ It was this 'changed' fauna that probably began dispersing northward across the Indomalaysian route as Asian forms spread south when the Australian 'ferryboat' (McKenna, 1973) neared its Asian 'dock'.

In conclusion, then, I would reopen consideration of the origins of the non-passeriform avifauna of Australia and call for a re-evaluation of over 40% of that fauna as data increases, particularly that regarding phylogeny of avian groups and the fossil record in Australia. Then, and only then, can probabilities be estimated that favour either an Indomalaysian or an Antarctic route for those groups in question.

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¹³ Such severe climatic changes taking place in the Australian Tertiary may serve as yet another factor, in addition to those mentioned by Keast (1972), that accounts for the differences in the diversity and endemism characteristic of the South American, African, and Australian avifaunas. Both the South American and the African land masses have remained at nearly the same latitudinal positions throughout the Tertiary with concomitant stability of climatic regimes affecting those continents. Australia, on the other hand, has quite noticeably moved some 30-50° of latitude northwards. Perhaps such changes, and possibly accompanying extinctions, account in part for the lower endemism in Australia when compared to that characterizing South America as well as such factors as smaller land area, less topographic diversity, decidedly smaller areas of tropical environments, etc. suggested by Keast.

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